

INTRODUCTORY MYCOLOGY

Wiley Eastern University Edition

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INTRODUCTORY MYCOLOGY

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Affectionately dedicated to
my wife JULIET

for her help, her encouragement,
and her good disposition
throughout the progress of this task

PREFACE

Progress in mycology has been so pronounced in the last ten years, and the first edition of this book has been so kindly received by students and teachers throughout the world, that I have felt compelled to revise the text in accordance with newer findings.

The new edition is no different from the first in its general approach to the study of fungi. Morphology and taxonomy continue to form the basis of discussion. However, significant physiological and genetic knowledge is interwoven with the morphological and taxonomic wherever it can be discussed on an introductory level.

Rising costs of production have made it necessary to eliminate some of the features that seemed desirable in the first edition. Thus, the chapter on bacteria was regretfully omitted, and the summaries at the ends of the chapters were eliminated. For the same reason, the number of references has been kept relatively small.

Two features of the first edition which students particularly praised: the inclusion of derivations of mycological terms in the text, and the illustrated life cycles, are retained.

Although this book was originally written to serve an undergraduate course, it has been widely adopted as a text in graduate courses as well. This fact influenced my decision to deal with some subject matter at a higher level than in the first edition; to introduce new groups, such as the Labyrinthulales, the Hyphochytridiomycetes, and the Trichomycetes; and to document the text much more thoroughly.

In an essentially morphological-taxonomic book, the system of classification adopted is, of course, of considerable importance. The phylum Myxomycophyta is no longer recognized. The Acrasiales and Labyrinthulales are treated as orders of uncertain affinity and are not included in any class or division. The Myxomycetes and the Plasmodiophorales are treated as classes of the Division Mycota.

For many years mycologists have recognized that the Phycomy-

cetes are a heterogeneous group of fungi. In 1958 Sparrow pointed out that the aquatic Phycomycetes consisted of several distinct "galaxies" to which he gave names with class endings. These galaxies are here recognized as classes, and the concept is expanded to include the non-aquatic groups. Sparrow used the term Phycomycetes for one of these galaxies. I am substituting Oömycetes as a class name for this group. Phycomycetes has been so well established in its wider sense that to give it a new restricted meaning would be inadvisable. Furthermore, those who agree with the principle of this classification, but who prefer not to discard the Phycomycetes as a group, may treat the classes in this book as sub-classes under the class Phycomycetes.

In treating the Ascomycetes I have essentially followed Martin's new key in Ainsworth's *Dictionary of the Fungi*, deviating from it in certain places. I have adopted Luttrell's sub-classes: Hemiascomycetidae, Euascomycetidae, and Loculoascomycetidae, using name endings recommended by the code, and have retained his convenient sub-division of the Euascomycetidae into four series: Plectomycetes, Pyrenomycetes, Discomycetes, and Laboulbeniomyces. I have deviated from both Luttrell and Martin in retaining the name Sphaeriales for the order they call Xylariales and in recognizing the Clavicipitales.

The chapter on the Deuteromycetes has been considerably expanded to include a discussion of the parasexual cycle, to inform the student of the new and rapidly spreading ideas on the classification of the Hyphomycetes, and to give somewhat more attention to the medical fungi than was given in the first edition.

In my treatment of the Basidiomycetes I have followed Martin but have included the Sporobolomycetaceae in this class instead of in the Deuteromycetes.

Some of my colleagues will again regret the absence of phylogenetic diagrams and the very limited phylogenetic discussions. The more I study the fungi the more uncertain I become about their relationships. I prefer, therefore, not to share my burden with students who are just beginning the study of fungi.

I was fortunate in securing once again the talented services of Dr. Sung Huang Sun, who prepared the drawings for both editions. I wish to express my appreciation to her and to those colleagues who furnished me with glossy prints of photographs or electron micrographs of fungi.

I owe special thanks to Professors Jules Brunel of the University of Montreal and Donald P. Rogers of the University of Illinois, who,

after reading the first edition from cover to cover, furnished me with long lists of comments, corrections, and suggestions, and to Professor Ralph Emerson of the University of California for his list of suggestions regarding the treatment of the lower fungi. I am particularly grateful to Professor G. W. Martin of the University of Iowa for his suggestions on the section dealing with the Heterobasidiomycetidae and for his willingness to take time on numerous occasions to discuss with me special problems on the classification of the fungi. From both teachers and students I shall continue to welcome suggestions which may help improve subsequent editions.

Once again my wife has been of the greatest help in judging the clarity of presentation. For her help, her encouragement, and her patience I am grateful.

CONSTANTINE J. ALEXOPOULOS

Austin, Texas
July, 1962

PREFACE TO THE FIRST EDITION

Ever since my student days, more than two decades ago, I have recognized the need for a textbook in Mycology written for the student who knows nothing about the fungi and who needs an orderly presentation of certain fundamental facts on the structure and classification of these organisms in the form of broad concepts and patterns, without the innumerable details and exceptions which make the study of fungi so fascinating for the specialist, but so bewildering for the beginner.

With the discovery of antibiotics, with the recent strides in the genetics and the biochemistry of the fungi, and with the realization of the role which fungi play in the causation of allergies and parasitic diseases of man, the need for a textbook written on the elementary level has become greater rather than less, for some knowledge of mycology is now not only necessary to the biologist in general, but is becoming a part of the cultural background of every educated and well-informed individual. It should be possible then to give the student an insight into the importance of fungi to man and into the structure, life history, and classification of the fungi in general without "telling all."

Although few people dispute, I believe, the need for an elementary text in this field, there is certainly no agreement as to the general approach which such a text should take. This, of course, is the age of biochemistry. The physiological and ecological approach is in vogue all the way from the kindergarten to the university, and function has replaced structure as the *raison d'être* of biological teaching. This, of course, is as it should be except for the undisputed fact that a beginning student understands function only through the structural

features associated with function. He does not see photosynthesis; he sees leaves, oxygen bubbles, and, eventually, chloroplasts; he does not see parasitism; he sees hyphae among host cells, haustoria which have invaded the cells, and symptoms in the form of leaf spots, twig cankers, or skin lesions, and sores; he does not see percentages of oxygen, nitrogen, phosphorus, and carbon, but rather the fascinating streaming of the plasmodium of *Physarum polycephalum* and *Fuligo septica*; he does not see genes A and a, but rather the two colonies which grow together and form the zygosporangia of *Phycomyces* or the ascocarps of *Neurospora*. In order for function to have any concrete meaning—and remember, we are speaking of the beginning student—a knowledge of general structure and probable relationships, and a working knowledge of terminology, the language of the science, it seems to me, are essential. In this book, therefore, I have discussed the structure of the fungi with stress on the life histories of various representative organisms and have given the basis of what to me appears to be the most acceptable system of classification, with some general remarks concerning the probable relationships of the major fungal groups. The purpose of this book then is to answer as simply and concisely as possible the question: "What are fungi and how do they affect us?" for the student in agriculture, bacteriology, or other general field of knowledge who has no time and, at this stage of his training at least, no desire to enter into the intricate details of Mycology. I hope that this book also will provide a background, such as can be given in a one-term introductory course for which it is designed, for the student who wishes to make the study of the fungi and their activities his life's work. This book is not a complete treatise on the fungi, and is not intended as a reference book.

So much for the reasons which prompted me to undertake this task. Now a few words in defense of the organization of this book. The chapter on bacteria, which may seem out of place in a book of this type, was included at the express request of a number of my students who think that a brief survey of our knowledge of the structure of bacteria would be at least as useful and as fully justified in a text on Introductory Mycology, as are the chapters on molds and yeasts invariably included in Introductory Bacteriology texts. Certainly I feel that a brief discussion of the Actinomycetes is essential, in view of the great role which these organisms appear to play in the economy of nature and of man, and in view of the fact that they provide a possible link between the bacteria and the fungi upon which it is interesting to speculate.

The chapter on slime molds is included because these organisms

are traditionally studied in Mycology and particularly because their intricate structure and great beauty are always sources of interest to the student.

The Deuteromycetes are discussed immediately after the Ascomycetes instead of at the very end of the book as has been customary in other books on Mycology. The dual naming and classification of the Ascomycetes is a difficult concept to teach to beginners and can be taught much better if the classification of the Deuteromycetes is discussed while the imperfect stages of the Ascomycetes are being studied, and if the Deuteromycetes themselves—those without a perfect stage—are discussed immediately afterward.

The inclusion of the derivations of mycological terms in the text at the time such terms are first introduced and defined rather than in the glossary alone is admittedly experimental. However, the opinion of a number of students consulted is that the advantage of such inclusions as aids in understanding the meaning of the terms far outweighs the possible disadvantage of temporary breaks in thought which parenthetical intrusions may cause.

A feature of the book which I hope will be especially helpful to the beginner is the inclusion of illustrated life cycles for a great many of the species discussed. Although such arrangement of figures requires more space and therefore necessitates a greater reduction in size of the individual drawings than other arrangements, the advantage gained by the presentation of the entire life cycle at a glance more than compensates for the sacrifice in size.

On the subject of classification, I aim to be as conservative as possible when insufficient knowledge of structure and relationships does not warrant acceptance of newer systems of classification, but as modern as possible where newer knowledge has made it advisable to discard older concepts even though such concepts may be well established in the literature. Thus, in the Phycomycetes, I have discarded the Archimycete-Oömycete-Zygomycete concept in favor of the classification based on flagellation, as adopted by Sparrow, Bessey, and Karling. It is my understanding that most Phycomycete specialists in this country have adopted this system. The choice of a classification system for the Ascomycetes was a more difficult task. I have recognized the old and convenient subdivision of the class into two subclasses, the Protoascomycetes and the Euascomycetes, and the subdivision of the latter into Plectomycetes, Pyrenomycetes, and Discomycetes. I have placed the Erysiphales in the Pyrenomycetes because of the arrangement of their asci in the cleistothecium; many mycologists include them in the Plectomycetes. In

treating the Pyrenomycetes, I have followed conservative lines. The main deviations from the traditional system are represented by the inclusion of the Mycosphaerellaceae and the Pleosporaceae in the Pseudosphaeriales rather than in the Sphaeriales, and by the transfer of the Phyllachoraceae—following Miller—to the Sphaeriales. Nannfeldt's classification has been adopted for the Discomycetes except for the inclusion of the family Sclerotiniaceae which most American mycologists now recognize. The traditional subdivision of the Basidiomycetes into Hemibasidiomycetes and Holobasidiomycetes has been followed. The former are discussed under four orders. The Holobasidiomycetes are treated rather briefly. To discuss them more thoroughly would necessitate the introduction of very detailed and difficult material which, I feel, should be left for the more advanced student of Mycology.

Controversial material on classification is introduced at times in order to point out to the student that there are other views on classification besides those which I have adopted, but controversial material is kept at a minimum in order to avoid confusion. I have tried to keep in mind that the student who will use this book will be struggling with a difficult, new terminology and with a mass of new facts, and that, at this stage of his training, he will not be ready to shoulder the burdens of the intended specialist. For this reason, phylogenetic discussion also has been kept at a minimum, but enough is introduced to indicate that we do have some definite, if not always agreed upon, ideas on the origin and evolution of the fungi.

On the matter of references, my policy has been to include: (1) all those cited in the text; (2) all those from which illustrations have been taken; and (3) a few of the most recent articles pertaining to the subject matter in each chapter—even though they may not have been mentioned in the text—to give the interested student a good start toward bibliographical work on any given phase. Very few references in foreign languages have been included. I should be the last person to deny the value of a knowledge of as many foreign languages as possible in the training of a scientist; but the value of foreign languages and the importance of reading foreign journals do not alter the fact that the American undergraduate who can read a language other than English is indeed unusual. The same is unfortunately true of most graduate students who have not reached the stage of passing the dreaded language examinations which, fortunately, are still required for the Ph.D. degree by most of our graduate schools.

I wish to express my sincere appreciation to all who have aided

me in any way. I am especially grateful to my wife, who has given me so many hours, which she would normally devote to her own profession, studying and criticizing the manuscript for clarity of statement and logic of presentation. She has been of the greatest possible help and inspiration throughout the entire task of writing this book. I am thankful to Professor Benjamin Hickok of Michigan State College, who read the entire manuscript and who made numerous editorial suggestions for its clarification. My sincere thanks go to Dr. E. D. Devereux of Michigan State College, who read the chapter on bacteria; to Dr. Leland Shanor of the University of Illinois, who read the chapters on Myxomycophyta and Phycomycetes; and to Dr. Lewis Wehmeyer of the University of Michigan, who read the chapters on Ascomycetes and Deuteromycetes. I alone, however, am responsible for the errors which may be found in this book, and for the views expressed on controversial material. My thanks also go to Mr. Nicholas Mizeres, formerly Assistant in Zoology at Michigan State College, who read the first draft of the manuscript while he was enrolled in my Introductory Mycology course, and who criticized it from the student's viewpoint.

Professors F. C. Strong, E. A. Bessey, and E. S. Beneke of Michigan State College, and Professor J. Arthur Herrick of Kent State University, have generously contributed a number of excellent color transparencies from which black and white negatives were made. Mr. Philip G. Coleman has taken a number of photographs especially for this book. To all the above I express my gratitude. I am grateful also to all authors of mycological articles who have given me permission to copy illustrations from their respective publications—particularly to those who have furnished me with glossy prints—as well as to the managers, editors, or publishers of the journals or books in which such illustrations have appeared. In order to avoid lengthy and cumbersome legends which would detract from the value of the illustrations in an introductory text, all credit lines for illustrations have been assembled under the section "Acknowledgments" which follows the Glossary at the end of the book. I wish to extend my thanks to The Science Press, W. B. Saunders Co., Torrey Botanical Club, McGraw-Hill Book Co., Inc., and The Macmillan Co. for permission to use the quotations which appear on pages 50, 50, 75, 124, 320, respectively. Individual credit lines for these quotations appear as footnotes on the pages on which the quotations are used.

Finally I wish to express my appreciation to Mrs. Sun Huang Sung, formerly Assistant in Botany, Michigan State College, who prepared all the original drawings and who also made all copies from pub-

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CONST. J. ALEXOPOULOS

Michigan State College
January 14, 1952

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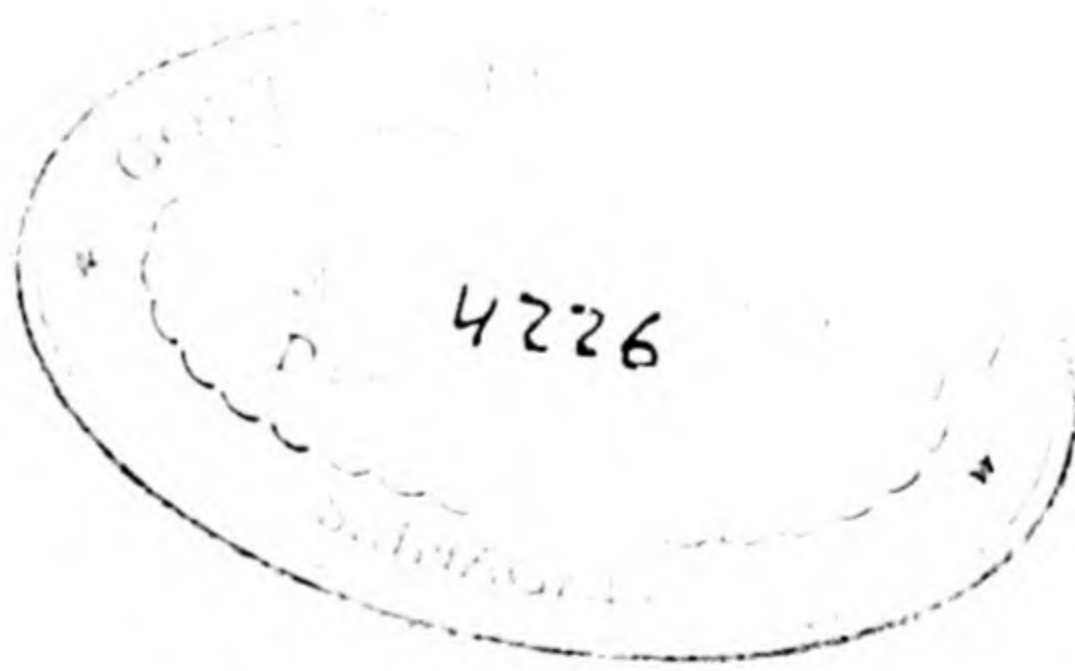
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PART I INTRODUCTION



1 THE FUNGI

molds, mildews, yeasts,
mushrooms, and puffballs

Three and one-half millennia ago, so the legend goes, the Greek hero Perseus, in fulfillment of an oracle, accidentally killed his grandfather Acrisius, whom he was to succeed on the throne of Argos. Then, according to Pausanias,¹ "When Perseus returned to Argos, ashamed of the notoriety of the homicide, he persuaded Megapenthes, son of Proetus, to change kingdoms with him. So when he had received the kingdom of Proetus he founded Mycenae, because there the cap (*mykes*) of his scabbard had fallen off, and he regarded this as a sign to found a city. I have also heard that being thirsty he chanced to take up a mushroom (*mykes*) and that water flowing from it he drank, and being pleased gave the place the name of Mycenae."²

Thus, one of the greatest civilizations that man has developed—the Mycenaean—may have been named for a legendary mushroom. Derived from the same Greek word, **mycology** (Gr. *mykes* = mushroom + *logos* = discourse), etymologically, is the study of mushrooms. And indeed that is how mycology began in the dim past, for the mushrooms are among the largest of fungi and attracted the attention of naturalists before microscopes or even simple lenses had been thought of. With the invention of the microscope by van Leeuwenhoek in the seventeenth century the systematic study of fungi began, and the man who deserves the honor of being called the founder of the science of mycology is Pier' Antonio Micheli, the Italian botanist who, in 1729, published *Nova plantarum genera*, in which his researches on fungi were included.

But what are fungi? To define the exact limits of the group is

¹ See Frazer's translation (1898) of Pausanias; Ramsbottom, 1953.

² Quoted by permission of Macmillan and Co., London.

virtually impossible, for the more we study living organisms the more meaningless become our attempts to delimit any particular group. At present, biologists use the term *fungus* (pl. *fungi*; L. *fungus* = mushroom) to include *nucleated, spore-bearing, achlorophyllous organisms which generally reproduce sexually and asexually, and whose usually filamentous, branched somatic structures are typically surrounded by cell walls containing cellulose or chitin, or both.*

In simpler words, this means that fungi have, without a doubt, typical true nuclei in their cells, that they reproduce by means of spores, and that they have no chlorophyll. It means further that most fungi possess some sort of sexual mechanism, that they have thread-like bodies which usually branch, and that these tubular threads have cell walls which contain cellulose or chitin, or both these substances. This is perhaps as good a definition as any, but, like all definitions, it is not water-tight. Some true fungi, for example, are not filamentous, and the filaments of a few others have no cell walls. Some true algae, because they have lost their chlorophyll through evolution, fit the above definition rather well, but they are not fungi. Then there are some organisms which mycologists have studied, more or less by default, but which are probably not fungi. Such are the cellular slime molds and the so-called net slime molds.

In this book, then, we shall study mainly the molds and the mildews, the yeasts, the rusts and the smuts, the mushrooms and the puffballs, and all the other groups which we usually include in the fungi. We shall also devote some time to the slime molds, which are closely related to the true fungi, and we shall discuss very briefly the cellular slime molds and the net slime molds, two groups which we exclude from the fungi, but which mycologists often study.

Importance of Fungi to Man. The systematic study of fungi is only 250 years old, but the manifestations of this group of organisms have been known to man for thousands of years—ever since the first toast was proposed over a shell full of wine, and the first loaf of leavened bread was baked. Yet, even today, in a science-conscious world, a world in which the nucleus of the atom has become a household word, few people realize how intimately our lives are linked with those of the fungi. It can be said truthfully that scarcely a day passes during which all of us are not benefited or harmed directly or indirectly by these inhabitants of the microcosm. Mycologists are indeed poor propagandists.

Fungi play such an important role in the slow but constant changes

taking place around us because of their ubiquity and their astonishingly large numbers. Specifically, fungi are the agents responsible for much of the disintegration of organic matter, and as such they affect us directly by destroying food, fabrics, leather, and other consumers' goods manufactured from raw materials subject to fungal attack; they cause the majority of known plant diseases, and many diseases of animals and of man; they are the basis of a number of industrial processes involving fermentation, such as the making of bread, wines, beers, the fermentation of the cacao bean, and the preparation of certain cheeses; they are employed in the commercial production of many organic acids and of some vitamin preparations, and are responsible for the manufacture of a number of antibiotic drugs, notably penicillin. Fungi are both destructive and beneficial to agriculture. On the one hand they are responsible for millions of dollars' worth of damage to crops by causing plant disease, while on the other they increase the fertility of the soil by inducing various changes which eventually result in the release of plant nutrients in a form available to green plants. Finally, to introduce an epicurean theme, we must not overlook the delights of a thick, juicy steak "smothered"—as the chefs would have it—with the fructifications¹ of *Agaricus campestris bisporus*, the cultivated mushroom.

The fungi are no longer the private concern of the mycologists. Cytologists, geneticists, and biochemists have found that fungi can be important research tools in the study of fundamental biological processes. Because of the rapidity with which some fungi grow and reproduce, a much shorter time is required to obtain a number of generations of fungi than of higher plants or animals. Furthermore, the fact that fungal spores produced by meiosis will grow into haploid individuals gives geneticists an opportunity for direct and rapid tetrad analysis. In addition, fungi, which can be grown in test tubes, require less space and less expensive equipment than most higher plants and animals.

The red bread-mold *Neurospora* is a case in point. C. L. Shear and B. O. Dodge, two eminent American mycologists of the U. S. Department of Agriculture, discovered this fungus in 1927 and pointed out the properties that make it an almost ideal organism for study of the laws of heredity. In a series of papers, Dodge then step by step laid the foundations of a new branch of science which has come to be known as haploid genetics. Geneticists and biochemists, alerted by Dodge's discoveries, began using *Neurospora*

¹ In mycology we use the terms *fructification* and *fruiting body* to designate any structure that contains spores. For the definition of a spore see page 13.

as an experimental tool. A series of researches followed which brought out the manner in which genes control enzymes, and elucidated the biochemical pathways which operate in living organisms. The slime molds too are being widely used in research. For a long time, they were the property of the mycologists alone. Then cytologists, biochemists, and biophysicists found *Physarum polycephalum* to be an excellent experimental organism for the study of the mitotic cycle, of morphogenesis, and of the causes and the mechanism of protoplasmic streaming.

Undoubtedly many more fungi have contributions to make to the knowledge and, consequently, the welfare of man. Some are already known; others await discovery. It is the mycologists who will find them!

General Characteristics. The fungi constitute a group of living organisms devoid of chlorophyll. They resemble green plants in that, with few exceptions, they have definite cell walls, they are usually non-motile, although they may have motile reproductive cells, and they reproduce by means of spores. They do not possess stems, roots, or leaves, nor have they developed a vascular system as have the more advanced types of plants. Fungi are usually filamentous and multicellular; their nuclei can be demonstrated with relative ease; their somatic structures, with few exceptions, exhibit little differentiation and practically no division of labor.

The filaments constituting the body of a fungus elongate by apical growth (Figure 1), but most parts of an organism are potentially capable of growth, and a minute fragment from almost any part of the fungus is sufficient to start a new individual. Reproductive structures are differentiated from somatic structures and exhibit a variety of forms, on the basis of which we classify the fungi. Few fungi can be identified if their reproductive stages are not available. With relatively few exceptions, the somatic parts of any fungus resemble those of many other fungi.

Nutrition and Growth. Fungi obtain their food either by infecting living organisms as parasites (Gr. *parasitos* = eating beside another), or by attacking dead organic matter as saprobes (Gr. *sapros* = rotten + *bios* = life). The majority of known fungi, whether normally parasitic or not, are capable of living on dead organic material, as is shown by the fact that we can grow them artificially on synthetic media.¹ Fungi which live on dead matter and are incapable of infecting living organisms are called obligate saprobes; those capable

¹ Substrata on which we culture fungi artificially. We use both liquid and solid media, the latter containing some solidifying agent, generally agar.

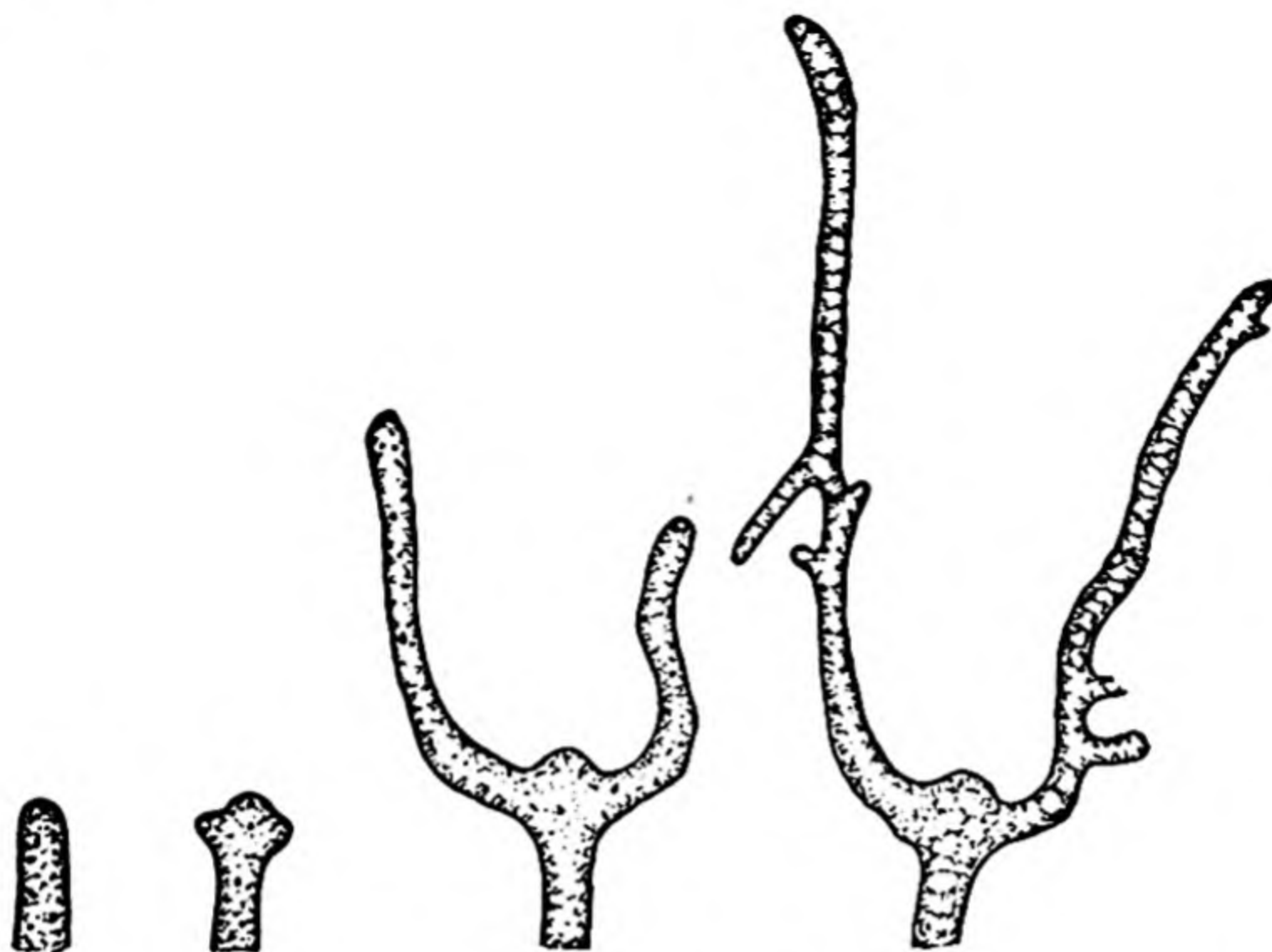


Figure 1. Successive stages of growth of a hyphal tip, drawn at half-hour intervals. (*Gelasinospora calospora* var. *autosteira*.)

of causing disease or of living on dead organic matter, according to circumstances, **facultative parasites** (or **facultative saprobes**); and those which cannot live except on living protoplasm, **obligate parasites**. A living organism infected by a parasite is known as the **host**. It is probable that, when we learn more about the physiology of the fungi, we shall be able to devise synthetic media on which to grow all the so-called obligate parasites.

The widespread association between fungal hyphae and the roots of higher plants is known as **mycorrhiza** (pl. **mycorrhizae**; Gr. *mykes* = mushroom + *rhiza* = root). In many instances both plant and fungus derive benefit from the association; in others, the fungus is clearly the parasite, but the injury to the host is negligible. If the balance is disturbed, however, the fungus may cause severe root disease. Much has been written about mycorrhiza (Kelley, 1950), but the exact relationship between the associates is still not understood.

Fungi differ from most plants in that they require already elaborated food in order to live, and are incapable of manufacturing their own. But if given carbohydrates in some form—preferably glucose, sucrose, or maltose—most fungi can synthesize their own proteins by utilizing inorganic or organic sources of nitrogen and various mineral

elements essential for their growth. Laboratory studies have established that C, O, H, N, P, K, Mg, S, B, Mn, Cu, Mo, Fe, and Zn are required by many fungi, probably by all. Other elements, such as Ga, are required by some. That Ca is also essential has not been definitely established but appears highly probable. As a general rule glucose is the best source of C, and organic N compounds the best source of N, with ammonium compounds and nitrates next in line. Many fungi are capable of synthesizing vitamins they require for growth and reproduction, as do other organisms. Some, however, are deficient in thiamine or biotin, or both, and must obtain these or their precursors from the substratum. Fungi usually store excess food in the form of glycogen or oil.

Different fungi have different food requirements. Some are omnivorous and can subsist on anything that contains organic matter. The common green mold (*Penicillium* sp.) and the common black mold (*Aspergillus* sp.), given a little moisture, will grow on anything from strawberry jam to shoe leather. Other fungi are more restricted in their diet; a few of the obligate parasites not only require living protoplasm for food, but also are highly specialized as to the species and even the variety of host they parasitize. The enzymes a fungus is capable of producing govern to a large extent its ability to utilize certain substances as food.

Most fungi will grow between 0° and 35° C., but optimum temperatures lie in the range of 20–30° C. The ability of fungi to withstand extremely low temperatures (as low as –195° C.) for at least a few hours has been demonstrated.

In contrast to bacteria, fungi prefer an acid medium for growth, a pH of 6 being near the optimum for most species which have been investigated.

Although light is not required for the growth of fungi, some light is essential for sporulation in many species. Light also plays a part in spore dispersal, the spore-bearing organs of many fungi being positively phototropic and discharging their spores toward the light. The classic researches of Buller on the relationship of light to spore dispersal make fascinating reading. They may be found in his *Researches on Fungi*, published between 1909 and 1950.

Somatic Structures. The fungal thallus typically consists of microscopic threads or filaments which branch in all directions, spreading over or within the substratum utilized for food. Each of these filaments is known as a *hypha* (pl. *hyphae*; Gr. *hyphe* = web). A hypha is made of a thin, transparent, tubular wall filled or lined with a layer of protoplasm varying in thickness. Depending on the species, the

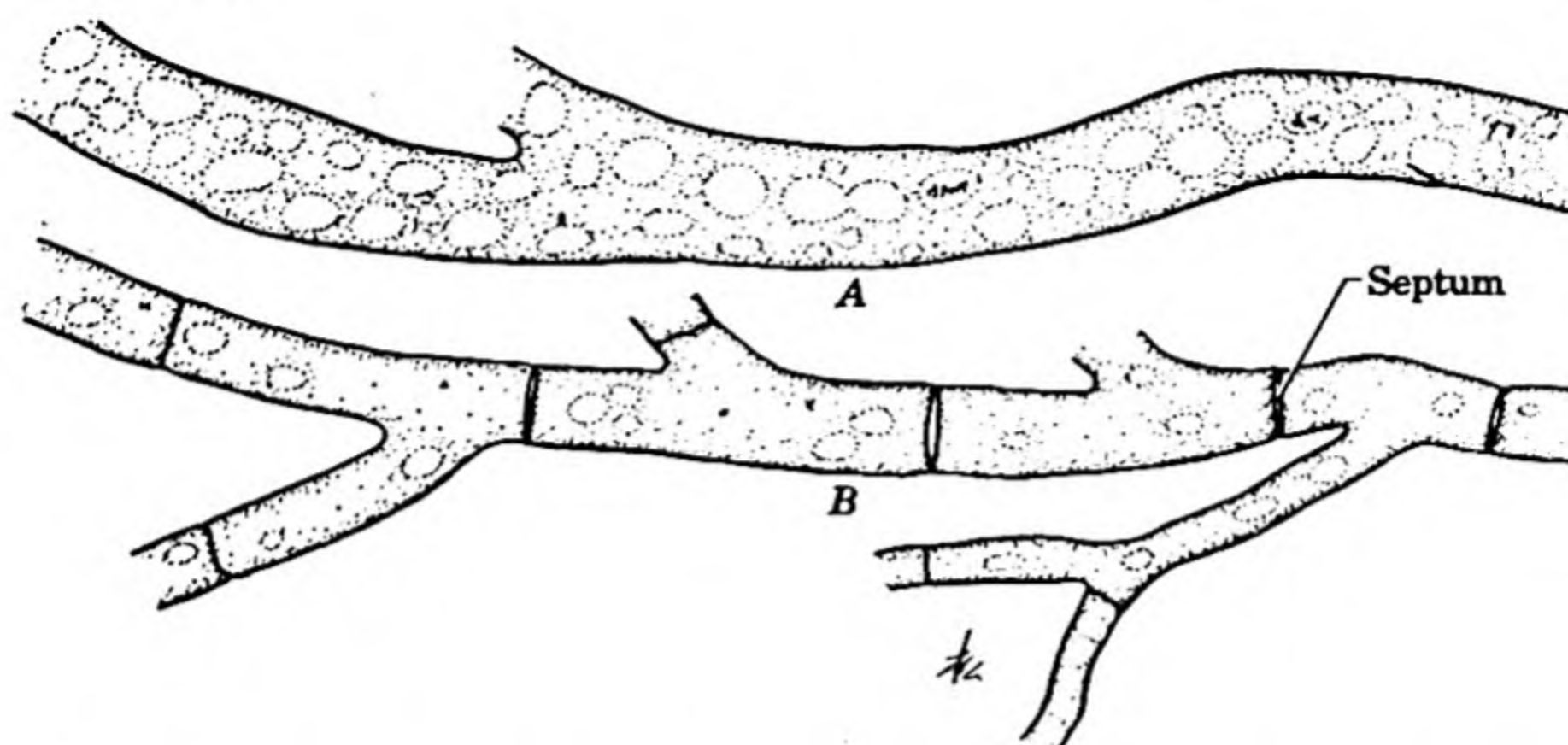


Figure 2. Somatic hyphae. A. Portion of a coenocytic (non-septate) hypha.
B. Portion of a septate hypha.

protoplasm may be continuous throughout or it may be interrupted at irregular intervals by partitions or cross-walls which divide the hypha into cells. The cross-walls are called *septa* (sing. *septum*; L. *septum* = hedge, partition) (Figure 2B). In septate forms, the protoplasts on each side of a septum are connected by living strands which pass through a central pore in the septum.

The chemical composition of the cell wall is not the same in all fungi. In some forms cellulose is probably the chief constituent. In most fungi, particularly in the higher forms, the cell wall is composed chiefly of chitin. Callose, a complex carbohydrate, lignin-like substances, and other organic materials have also been detected in many fungi. None of these materials occurs alone, the composition of the fungal cell wall being very complex and difficult to determine. Nor is the composition of the cell wall of any fungal species the same under all circumstances. On the contrary, substances which may be present in the young hyphae may disappear almost completely as the hyphae grow older, or other materials may be deposited and mask the presence of the earlier constituents, making their detection very difficult. Furthermore, it has been shown definitely that external factors, such as the composition of the media, pH values, and temperature, profoundly influence the composition of the fungal walls (Foster, 1949).

Fungi possess organized, demonstrable nuclei each with a nuclear membrane, a nucleolus, and chromatin strands which become organized into chromosomes during division (Figure 3). The nuclei

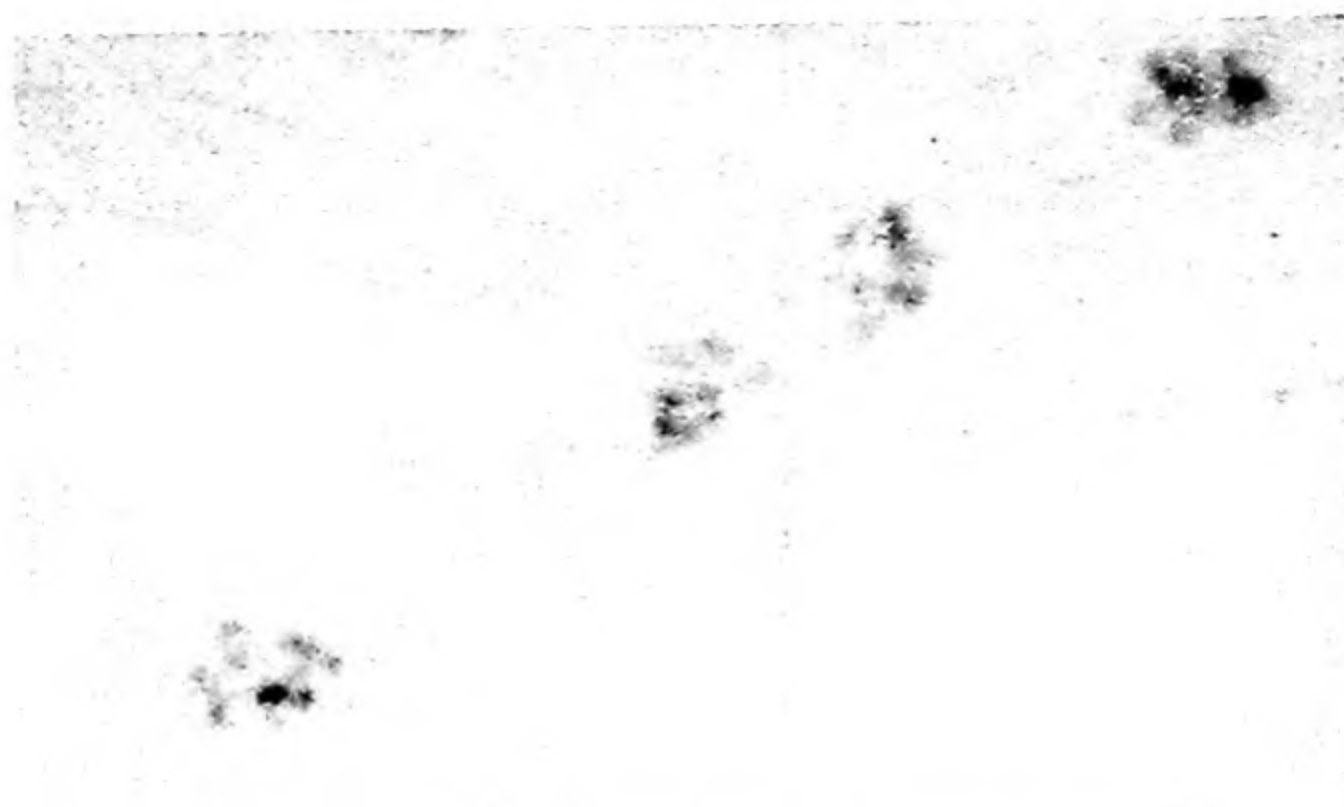


Figure 3. Fungal hypha with dividing nuclei showing chromosomes. (*Blastomyces dermatitidis*.) Courtesy A. Bakerspigel, 1959, *Can. Jr. Microbiol.*, 3:923-936.

in the somatic portions of most fungi are extremely minute, and their study is very difficult. At the present time, we do not know exactly how nuclear division occurs in the somatic structures. The researches of DeLamater (1950), Widra and DeLamater (1955), Ganesan (1959), Ganesan and Roberts (1959), and Ward and Curysek (1961) show that nuclei of yeasts and other fungi divide by ordinary mitosis. On the other hand, Robinow (1957), Bakerspigel (1957-1959 *a, b*), and Saksena (1961), who have studied nuclear division in the hyphae of a number of fungi distributed throughout the major categories, believe that somatic nuclei divide in a manner not directly comparable to mitosis in that no spindles or metaphase plates are formed (Figure 4). In specialized structures associated with the sexual cycle of the fungi, in which meiosis takes place, the nuclei are very much larger than the somatic nuclei. Mei-



Figure 4. Nuclear division in a fungal hypha. Arrow points to a double strand of chromatin. (*Schizophyllum commune*.) Courtesy A. Bakerspigel.

otic divisions are typical, with spindles and metaphase plates appearing no different from, if much smaller than, those of more advanced forms of life.

In fungi whose hyphae have no septa—we call them aseptate—the nuclei are embedded in the cytoplasm and are scattered more or less uniformly throughout its mass. This condition is termed **coenocytic** (Gr. *koinos* = common + *kytos* = a hollow vessel) (Figure 2A). The individual cells of septate hyphae may contain one, two, or many nuclei.¹ Uninucleate cells are characteristic of some fungi, binucleate cells of others, whereas multinucleate cells may occur in most. Vacuoles, oil droplets, and other inclusions also are commonly present in the cytoplasm.

The mass of hyphae constituting the thallus of a fungus is called the **mycelium** (pl. *mycelia*; Gr. *mykes* = mushroom). The mycelium of some of the higher fungi forms thick strands. In certain types of such strands—the **rhizomorphs** (Gr. *rhiza* = root + *morphe* = shape)—the unit hyphae lose their individuality and form complex tissues which exhibit a division of labor. The string-like mass has a thick, hard cortex, and a growing tip whose structure reminds us of that of a root tip. Rhizomorphs are resistant to adverse conditions and remain dormant until favorable conditions return. Growth is then resumed, the rhizomorph attaining great length.

The mycelium of parasitic fungi grows on the surface of, or more often inside, the host, either spreading between the cells or penetrating into them. If the mycelium is intercellular, food is absorbed through the host cell wall or membrane. If the mycelium penetrates into the cells, the hyphal walls come into direct contact with the host protoplasm. Intercellular hyphae of many fungi, especially of obligate parasites of plants, obtain nourishment through **haustoria** (sing. *haustorium*; L. *haustor* = drinker). Haustoria, which the fungus sinks into the plant host cells through a minute pore punctured in the cell wall, are outgrowths of the somatic hyphae. They are regarded as specialized absorbing organs. Haustoria may be knob-like in shape, elongated, or branched like a miniature root system (Figure 5). Haustoria are not produced in artificial culture by any fungus so far as anyone has determined. However, Dickinson (1949) has shown that certain obligate parasites will send haus-

¹ Regardless of the number of nuclei they contain, hyphal segments between septa are usually called cells. Strictly speaking however, a cell contains but a single nucleus, and the term **coenocyte** would describe more accurately a compartment with more than one nucleus.

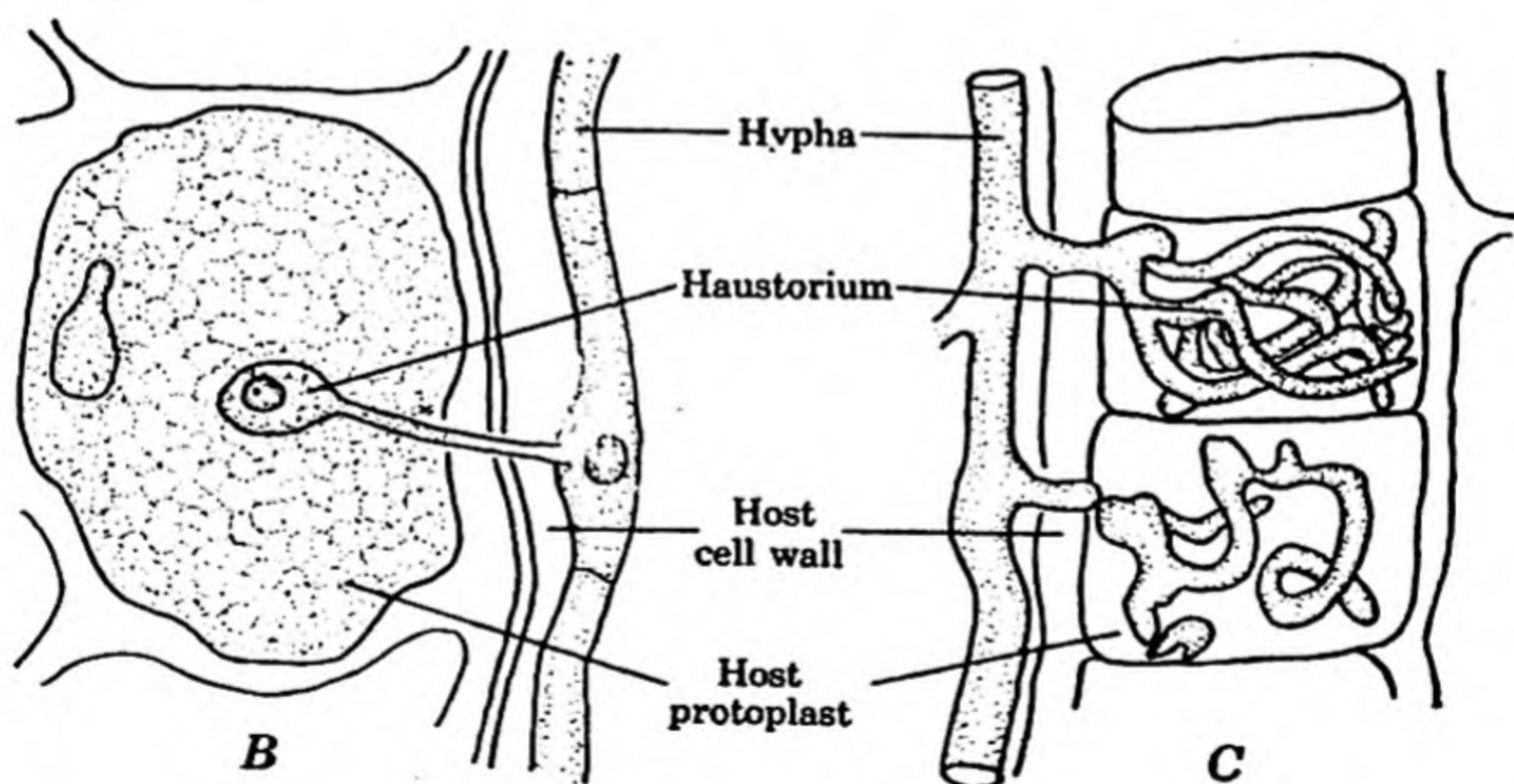
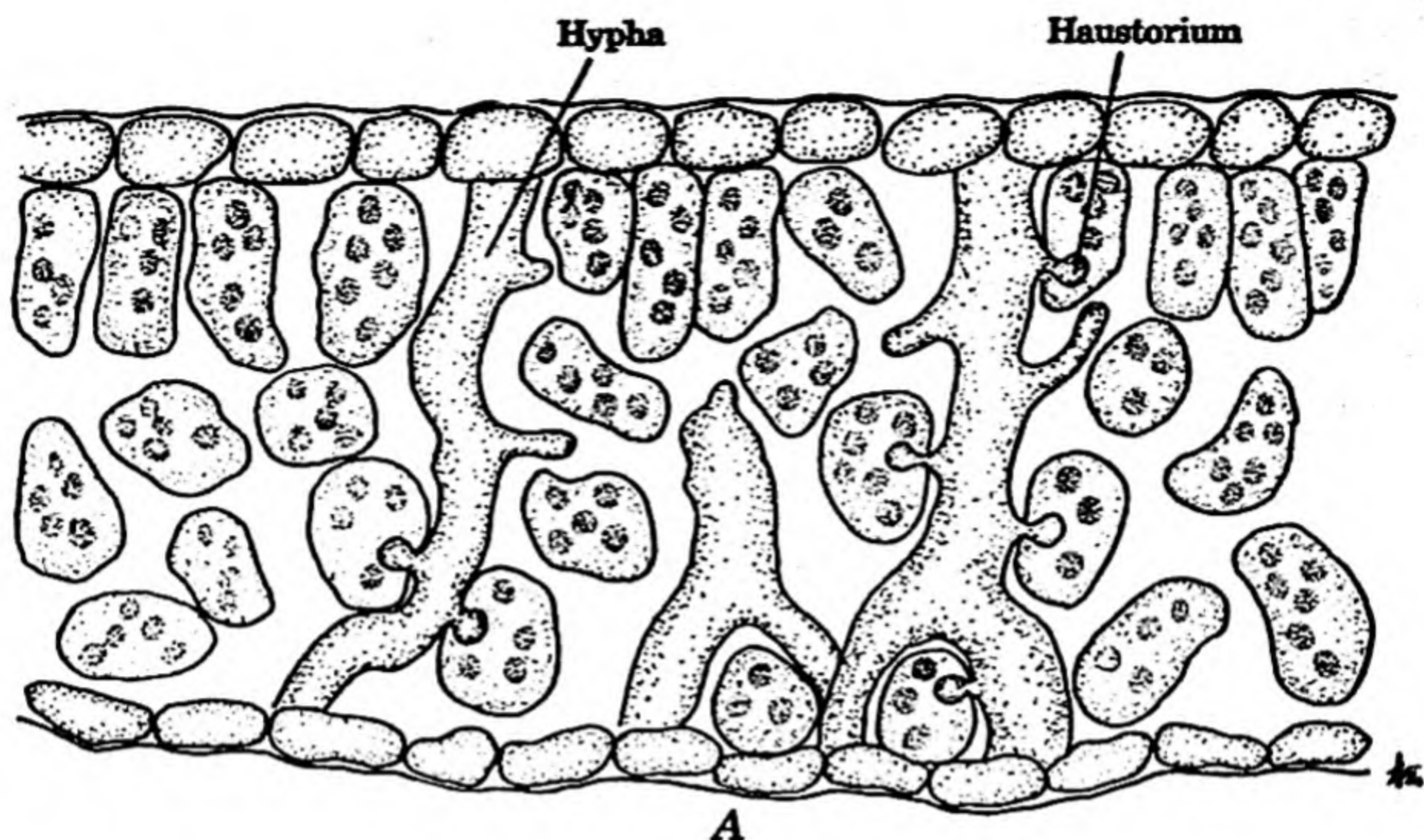


Figure 5. Three types of haustoria. *B*, redrawn from Smith, 1900, *Bot. Gaz.*, 29:153-184, by permission of the University of Chicago Press, Chicago; *C*, redrawn from De Bary, 1863, *Ann. sci. nat. Bot.*, 4 ser., 20:5-148.

toria through artificial membranes substituted for the epidermis of the host in which the fungus is growing. The production of haustoria is probably a response to the contact stimulus as well as to the stimulus of nutrients.

The hyphae of saprobic fungi come in intimate contact with the substratum and obtain food by direct diffusion through the hyphal walls, causing disintegration of the organic matter which they utilize. The older hyphae die as the mycelium grows and branches, and they themselves disintegrate because of the activities of other microorganisms which prey upon their dead bodies.

Fungal hyphae are capable of indefinite growth under favorable conditions. In nature, fungal colonies have been known to continue growing for 400 years or more. It is probable that some mycelia, *but not individual cells*, are thousands of years old.

The mycelium of a fungus generally begins as a short germ tube emerging from a germinating spore (Gr. *sporos* = seed, spore) (Figure 6). Spores are minute propagating units produced by most fungi, which serve in the production of new individuals of the same species. The mycelium of a fungus has a tendency to grow more or less equally in all directions from a central point, and to develop a spherical colony. You can observe this ideal situation in the laboratory by growing certain fungi in liquid media; a spherical, fluffy colony then develops around a particle of food, such as a grain of wheat or a portion of a hemp seed, placed in the water or other liquid media employed. An actual sphere is seldom formed in nature, however, because of the effect of external factors, such as the type of substratum, light, and chemicals, to which fungi readily respond. Fungal colonies tend to be circular in outline on solid media (Figure 10B).

During certain stages of the life history of most fungi, the mycelium becomes organized into loosely or compactly woven tissues, as distinguished from the loose hyphae ordinarily composing a thallus. We use the general term **plectenchyma** (Gr. *pleko* = I weave + *enchyma* = infusion, *i.e.*, a woven tissue) to designate all organized fungal tissues. We recognize two general types of plectenchyma: **prosenchyma** (Gr. *pros* = toward + *enchyma* = infusion, *i.e.*, approaching a tissue) is a rather loosely woven tissue in which the component hyphae lie more or less parallel to one another, and their typically elongated cells are easily distinguishable as such; **pseudoparenchyma**¹ (Gr. *pseudo* = false + *parenchyma* = a type of plant

¹ Unfortunately different authors have used these terms loosely and caused much confusion. I am using Ainsworth's *A Dictionary of the Fungi* (1961) as my authority in defining these terms.

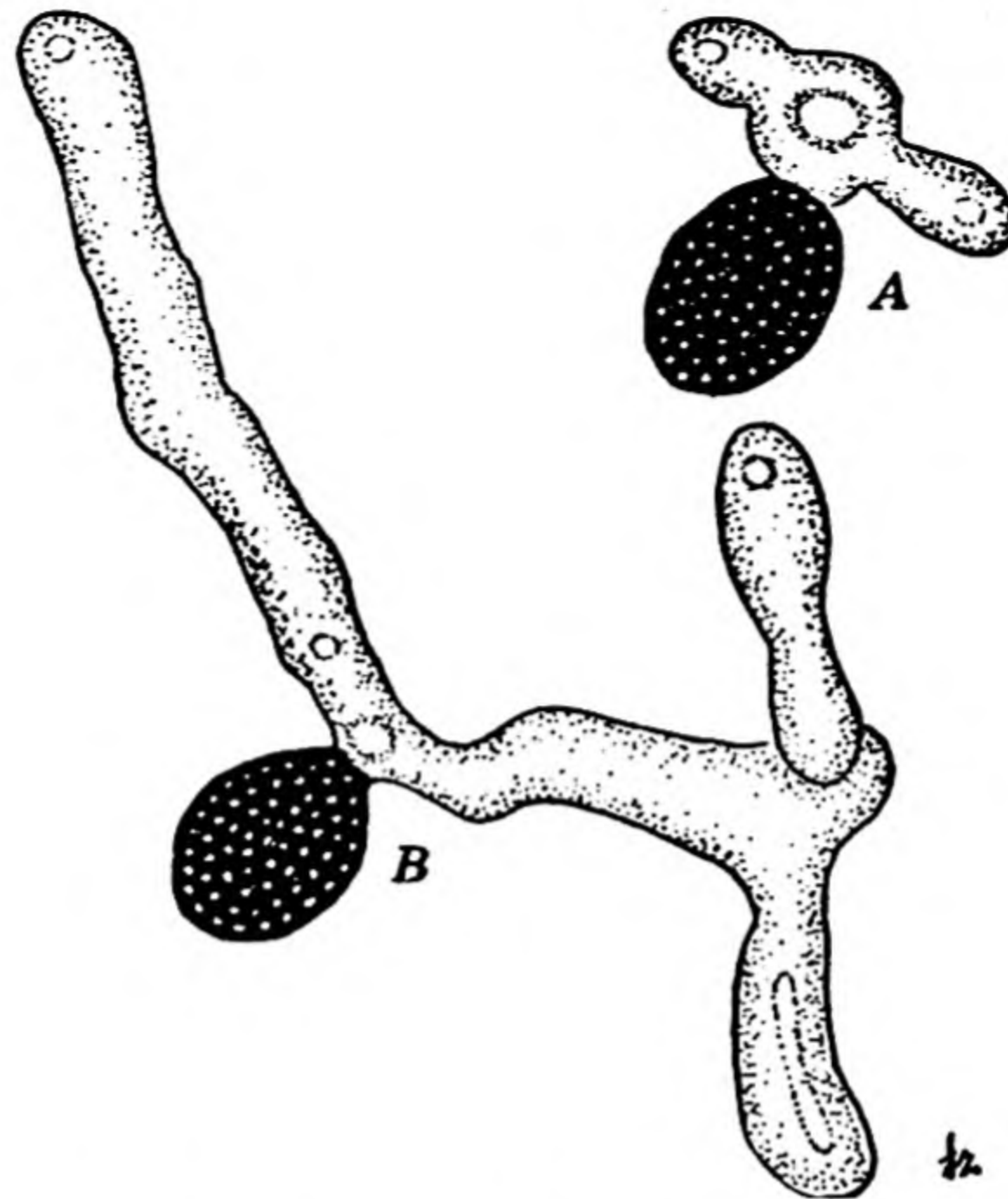


Figure 6. Two stages in the germination of a spore. *A.* Approximately 1½ hours after beginning of germination. *B.* Approximately 10 hours. (*Gelasinospora calospora* var. *autosteira*.)

tissue) consists of closely packed, more or less isodiametric or oval cells resembling the parenchyma cells of higher plants. In this type of fungal tissue, the hyphae have lost their individuality and are not distinguishable as such (Figure 7).

Prosenchyma and pseudoparenchyma compose various types of somatic and reproductive structures which many fungi form. Two such somatic structures are the **stroma** (pl. **stromata**; Gr. *stroma* = mattress) and the **sclerotium** (pl. **sclerotia**; Gr. *skleros* = hard). A stroma is a compact, somatic structure much like a mattress, on which or in which fructifications are usually formed (Figures 8A, B). A sclerotium is a hard resting body resistant to unfavorable conditions; it may remain dormant for long periods of time and germinate upon the return of favorable conditions (Figures 8C, D).

Reproduction. Reproduction is the formation of new individuals having all the characteristics typical of the species. Two general types of reproduction are recognized: **sexual** and **asexual**. Asexual reproduction, sometimes called somatic or vegetative, does not in-

volve the union of nuclei, sex cells, or sex organs. Sexual reproduction, on the other hand, is characterized by the union of two nuclei.

In the formation of reproductive organs, either sexual or asexual, the entire thallus may be converted into one or more reproductive structures, so that somatic and reproductive phases do not occur together in the same individual. Fungi which follow this pattern are called **holocarpic** (Gr. *holos* = whole + *karpos* = fruit). In the majority of fungi, however, the reproductive organs arise from but a portion of the thallus, while the remainder continues its normal somatic activities. The fungi in this category are called **eucarpic** (Gr. *eu* = good + *karpos* = fruit). The holocarpic forms are, therefore, less differentiated than the eucarpic and are regarded, for the most part, as more primitive.

Asexual Reproduction. Typically, fungi reproduce both asexually and sexually. In general, asexual reproduction is more important for the propagation of the species, since it results in the production of numerous individuals, and particularly since the asexual cycle is usually repeated several times during the season, whereas the sexual stage of many fungi is produced but once a year.

We sometimes define asexual reproduction as the non-sexual production of specialized reproductive cells such as spores. A broader definition, however, also includes any method of propagation of new

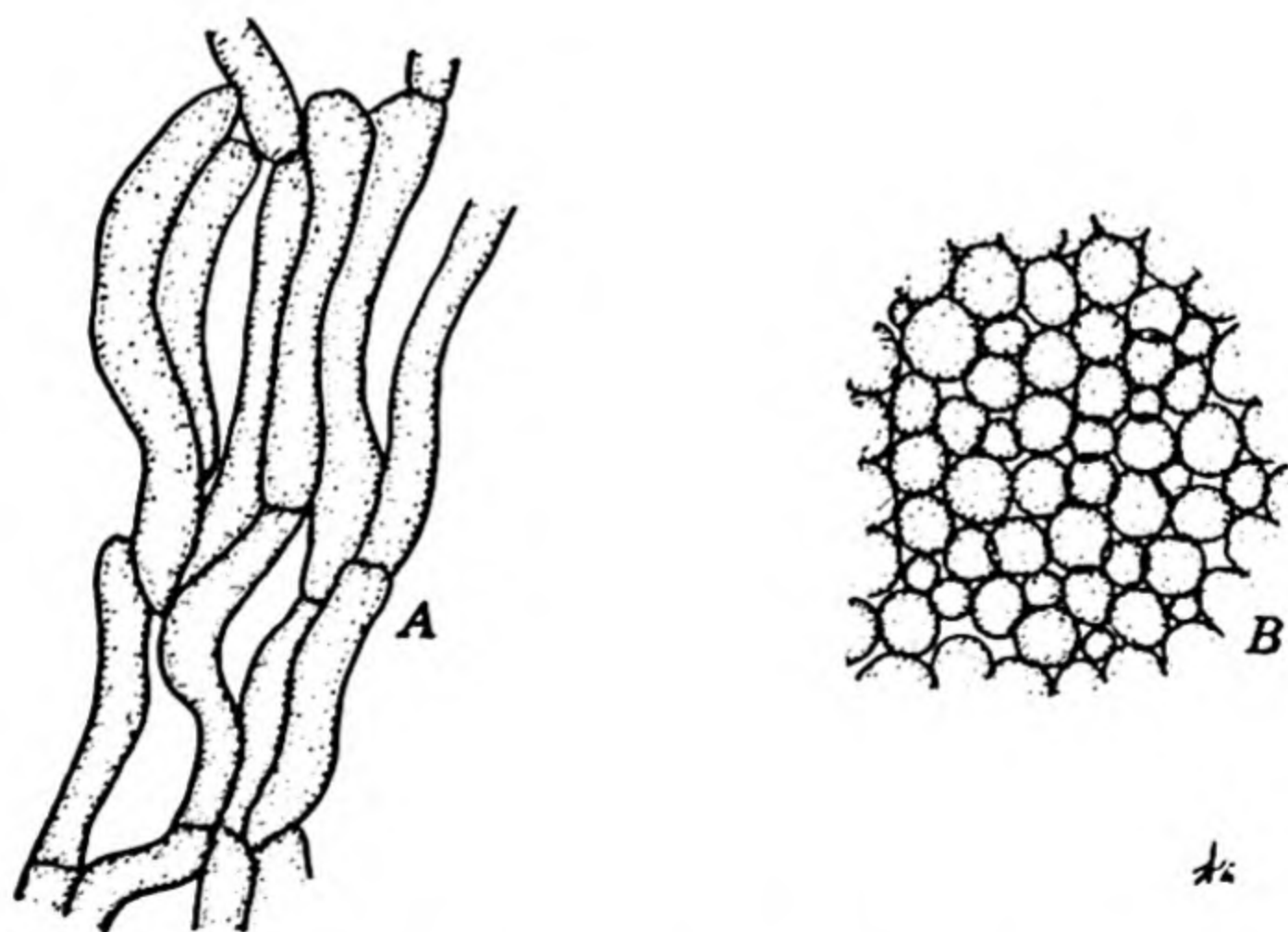


Figure 7. Fungal tissues (plektenchyma). A. Prosenchyma. B. Pseudoparenchyma.

individuals, such as simple division of a unicellular organism into two daughter cells, or of a multicellular thallus into a number of fragments each of which grows into a new individual. It is this broader concept of asexual reproduction that I am using here. In accord-

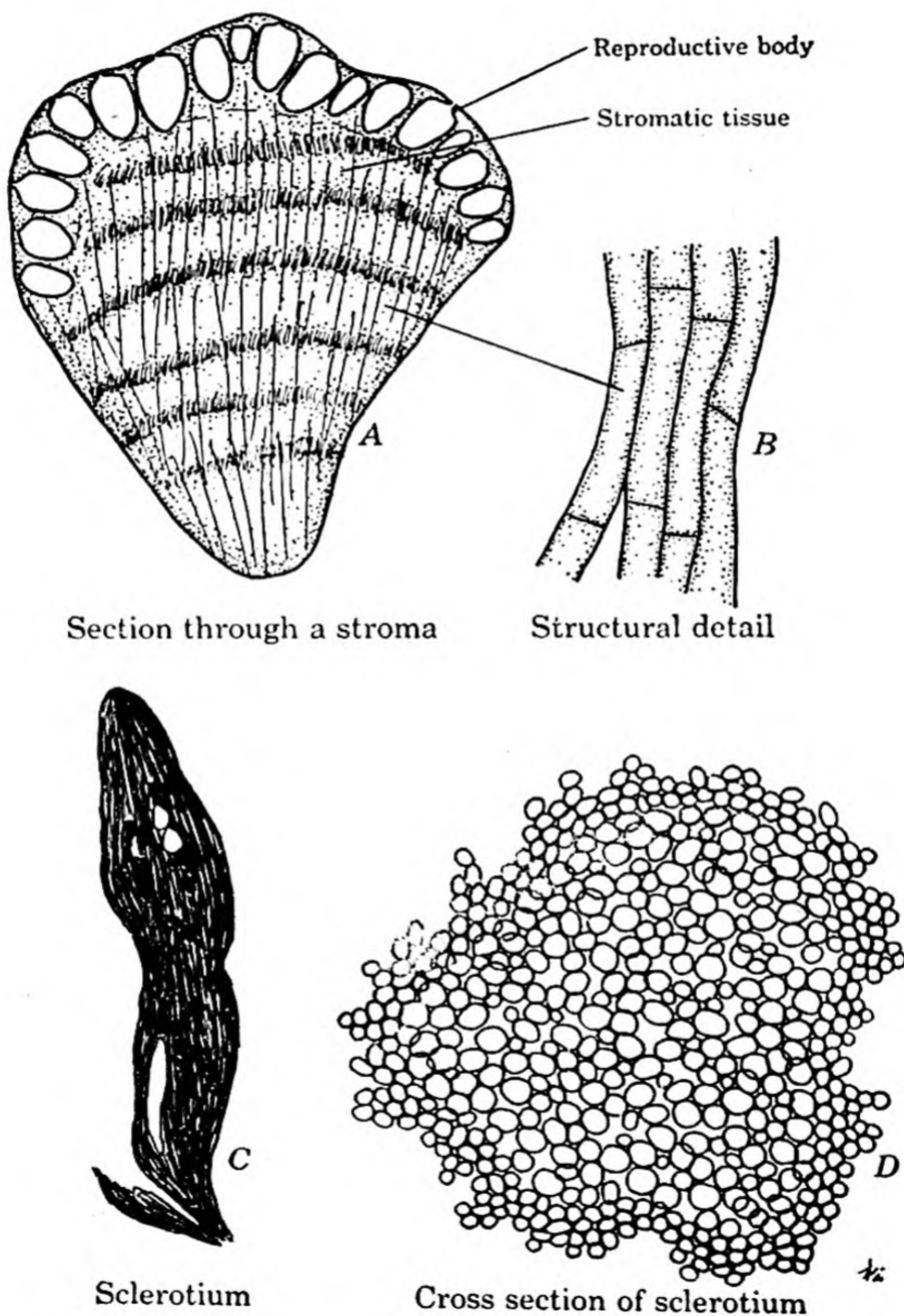


Figure 8. Stroma and sclerotium. A, B. *Daldinia* sp. C, D. *Claviceps purpurea*.

ance with this concept the asexual methods of reproduction commonly found in fungi may be summarized as follows: (1) fragmentation of the soma, each fragment growing into a new individual; (2) fission of somatic cells into daughter cells; (3) budding of somatic cells or spores, each bud producing a new individual; and (4) production of spores, each spore usually germinating to form a germ tube which grows into the mycelium.

Some fungi employ fragmentation of hyphae as a normal means of propagation. The hyphae break up into their component cells, now called *oidia* (sing. *oidium*; Gr. *oidion* = small egg) or *arthrospores* (Gr. *arthron* = joint, + *sporos* = seed, spore) (Figure 9A), which behave like spores. If the cells become enveloped in a thick wall before they separate from each other or from other hyphal cells adjoining them, they are called *chlamydospores* (Gr. *chlamys* = mantle + *sporos* = seed, spore) (Figure 9B). Fragmentation may also occur accidentally by the tearing off of parts of the mycelium through external forces. Such bits of mycelium under favorable conditions will start a new individual. Often in the laboratory we employ mycelial fragmentation to keep fungal cultures growing on artificial media by transferring a bit of mycelium to fresh media and thus starting a new colony (Figure 10).

Fission, the simple splitting of a cell into two daughter cells by constriction and the formation of a cell wall, is characteristic of the bacteria, and of some yeasts, which are true fungi (Figure 11A).

Budding is the production of a small outgrowth (bud) from a parent cell. As the bud is formed, the nucleus of the parent cell divides and one daughter nucleus migrates into the bud. The bud increases in size while still attached to the parent cell, and eventually breaks off and forms a new individual (Figure 11B). Chains of buds, forming a short mycelium, are sometimes produced. Budding takes place in the majority of yeasts, but it also occurs in many other fungi at certain phases of their life history or under certain conditions of growth.

The most common method of asexual reproduction in fungi is by means of spores. Spores vary in color from *hyaline*¹ (Gr. *hyalinos* = made of glass, i.e., colorless) through green, yellow, orange, red, brown, to black; in size, from minute to large; in shape, from globose through oval, oblong, needle-shaped to helical; in number of cells, from one to many; in the arrangement of cells; and in the way in

¹ It is unfortunate that the term *hyaline* is generally used as a synonym of "colorless." More correctly, it indicates a transparent object as opposed to an opaque one.

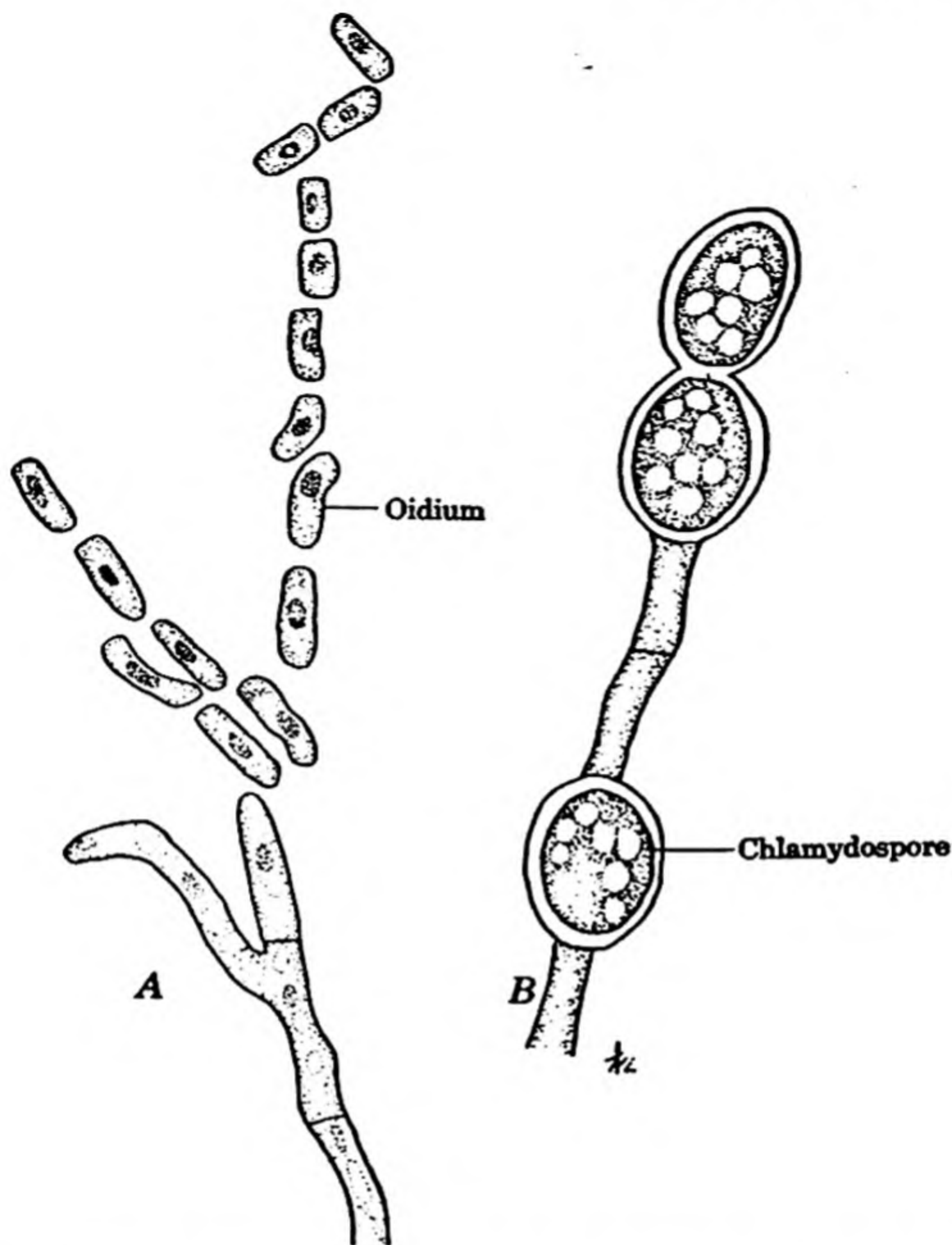


Figure 9. Asexual reproduction. A. Hypha fragmenting into oidia, also called arthrospores. (*Collybia conigena*.) B. Chlamydospores. (*Fusarium* sp.) A, redrawn from Kniep, 1917, *Zeitschr. Botanik*, 9:81-118.

which the spores themselves are borne (Figure 12). This infinite variety of spores makes the study of fungi particularly fascinating. Some fungi produce only one type of spore, whereas others produce as many as four types. Fungal spores produced asexually are either borne in **sporangia** (sing. **sporangium**; Gr. *sporos* = seed, spore + *angeion* = vessel) and are then called **sporangiospores**, or are produced at the tips or sides of hyphae in various ways and are then called **conidia** (sing. **conidium**; Gr. *konis* = dust + *-idion*, dimin. suffix).

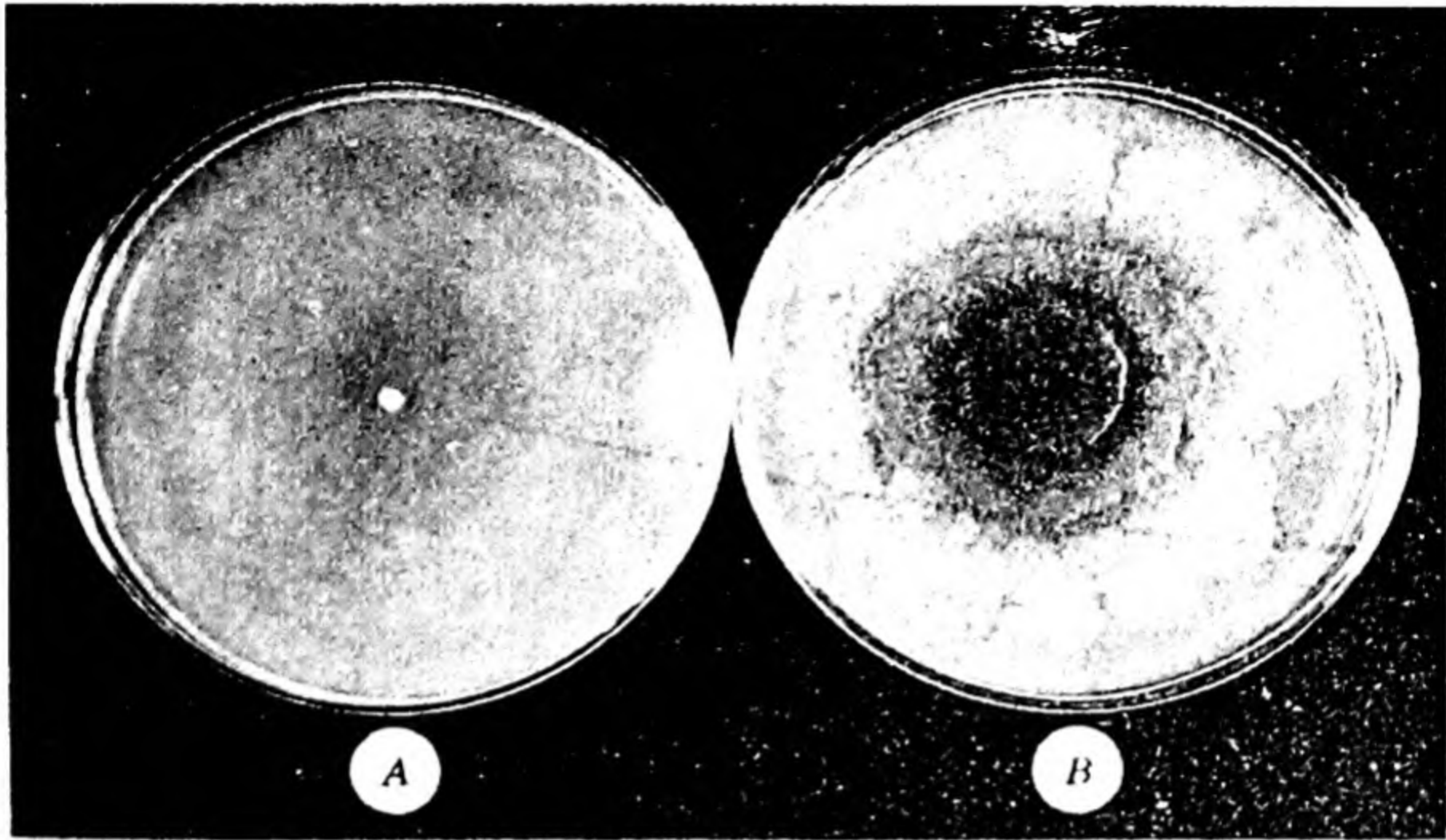


Figure 10. Mycelial fragmentation as employed in the laboratory for the propagation of fungi. *A.* Agar disc with fungous mycelium growing through it, cut from a colony and transferred to the surface of sterile agar. *B.* Resulting fungal colony 7 days after a disc similar to that in *A* was placed in the dish. Photograph by Philip G. Coleman.

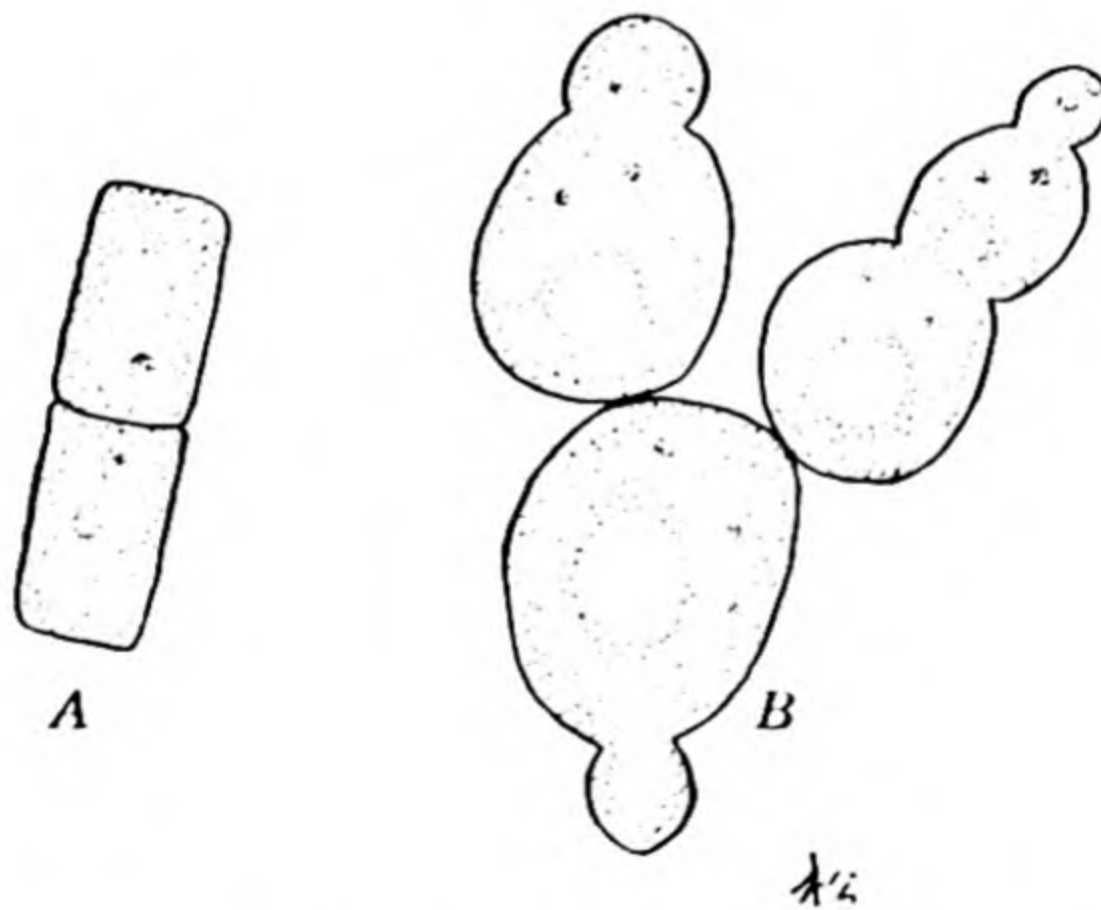


Figure 11. Asexual reproduction. *A.* Transverse cell division (fission). *B.* Budding.

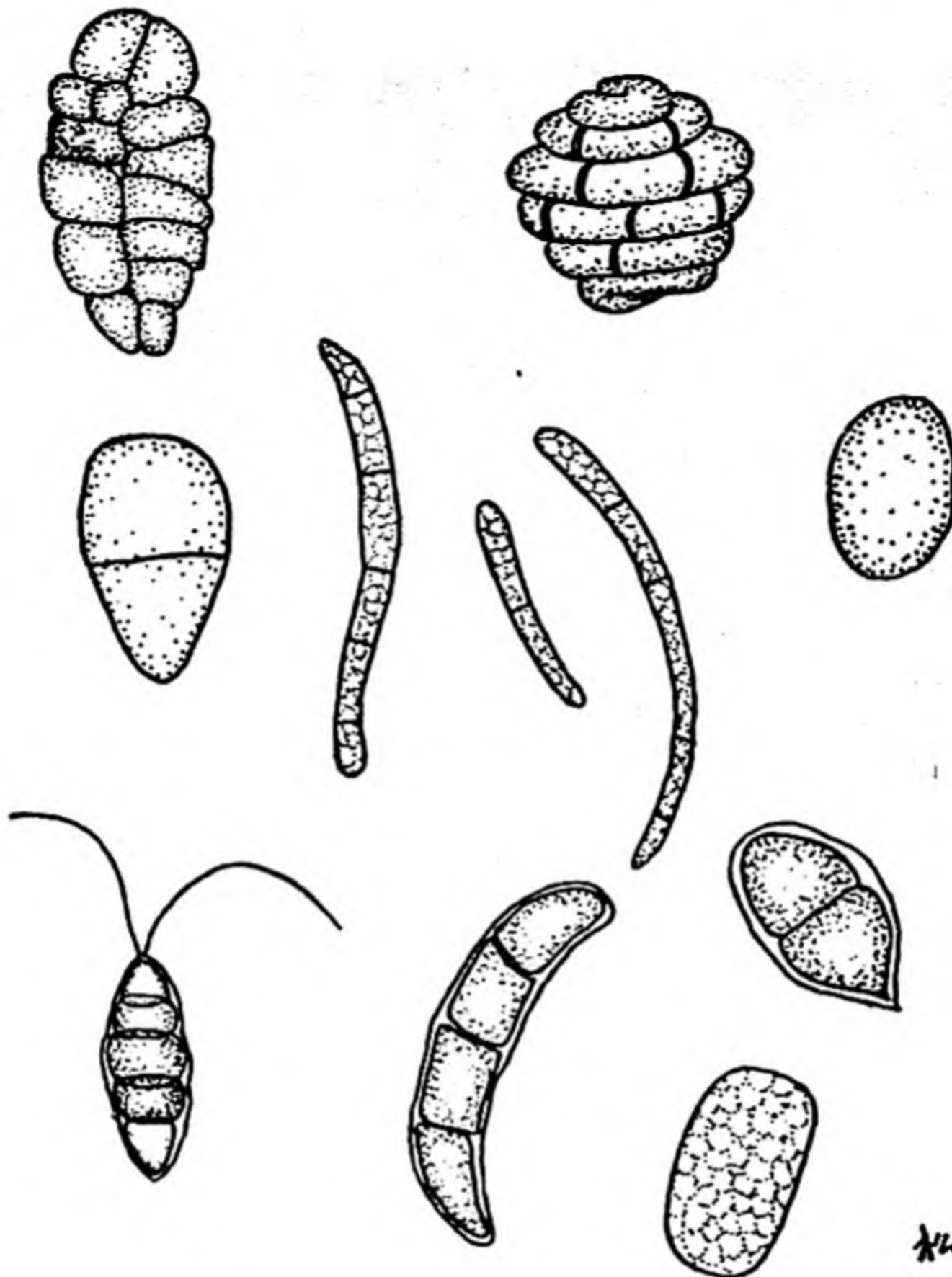


Figure 12. Asexual reproduction. Various types of fungal spores. Figure in upper right redrawn from Linder, 1929, *Ann. Mo. Bot. Gard.*, 16:227-388.

A sporangium is a sac-like structure whose entire contents are converted into one or more, usually many, spores. Sporangiospores may be motile or non-motile. In the lower fungi the sporangiospores are usually motile and are called **zoöspores** (Gr. *zoön* = animal + *sporos* = seed, spore). If non-motile they are called **aplanospores** (Gr. *a* = not + *planetes* = wanderer + *sporos* = seed, spore). Fungal zoöspores are equipped with one or two **flagella** (sing. **flagellum**; L. *flagellum* = whip). There are at least two types of flagella in the fungi: the **whiplash** and the **tinsel**. The whiplash flagellum is divided into two parts. The lower or basal portion is rigid and much longer than the upper or terminal portion, which is short and flexible. The tinsel flagellum is a feathery structure consisting

of a long rachis with lateral hair-like projections on all sides along its entire length (Figure 13).

The flagellar apparatus constitutes a very complex mechanism consisting of the flagellum itself, a blepharoplast (Gr. *blepharis* =

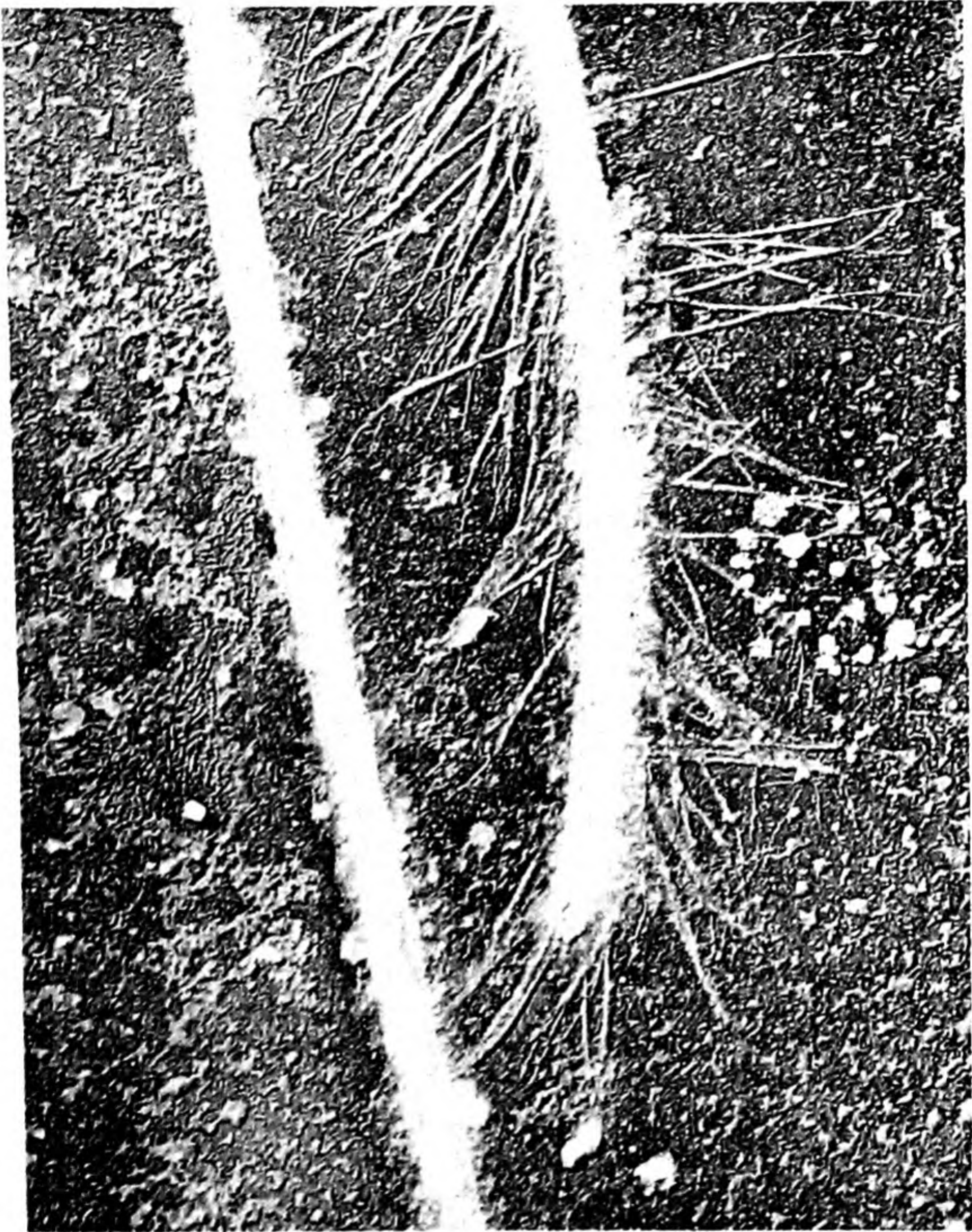


Figure 13. Part of a whiplash (*left*) and of a tinsel (*right*) flagellum. (*Phytophthora infestans*.) Courtesy Kole and Horstra, 1959, *Koninkl. Nederl. Akad. Wetensch. Proc.*, ser. C, 62:404-408, by permission of the Royal Dutch Academy.

eyelash + *plastid*), which is actually the base of the flagellum inside the motile cell, and a **rhizoplast** (Gr. *rhiza* = root + *plastid*), through which the flagellum is attached to the nucleus of the cell. The flagellum is composed of eleven parallel fibrils, nine peripheral fibrils forming a cylinder around two central ones. Each fibril is composed of subfibrils. In a whiplash flagellum, the two central fibrils are longer than the peripheral and extend farther out, forming the whip. The bases of the flagellar fibrils are doubled up within the zoöspore and form the blepharoplast (Koch, 1956). It is of great interest and importance that the general pattern of flagellum structure (*i.e.*, the 9 + 2 fibril construction) appears to be about the same in the flagellated cells of many organisms. This is true not only of the fungi, but of the algae, the mosses, the ferns, the protozoa, and the sperm cells of higher plants and animals as well. Of all the organisms so far investigated, only the bacteria differ in this respect. The bacterial flagellum appears to be composed of but a few strands or fibrils (perhaps only one) and may be the basic type of which all others are composed and from which all others have been derived.

The different types of conidia which the fungi produce—and there are many—we shall discuss in connection with the fungi which produce them.

Sexual Reproduction. Sexual reproduction in fungi as in other living organisms involves the union of two compatible nuclei. The process of sexual reproduction typically consists of three distinct phases. In the first of these, called **plasmogamy** (Gr. *plasma* = a molded object, *i.e.*, a being + *gamos* = marriage, union), a union of two protoplasts brings the nuclei close together within the same cell. The fusion of the two nuclei which are brought together by plasmogamy is called **karyogamy** (Gr. *karyon* = nut, nucleus + *gamos* = marriage) and constitutes the second phase of sexual reproduction. Karyogamy follows plasmogamy almost immediately in many of the lower fungi. In the higher fungi, however, these two processes are separated in time and space, plasmogamy resulting in a binucleate cell containing one nucleus from each parent. Such a pair of nuclei we call a **dikaryon** (NL. *di* = two + Gr. *karyon* = nut). These two nuclei may not fuse until considerably later in the life history of the fungus. Meanwhile, during growth and cell division of the binucleate cell, the dikaryotic condition may be perpetuated from cell to cell by the simultaneous division (conjugate division) of the two closely associated nuclei, and by the separation of the resulting sister nuclei into the two daughter cells. Nuclear

fusion, which eventually takes place in all sexually reproducing fungi, is sooner or later followed by **meiosis** (Gr. *meiosis* = reduction), which again reduces the number of chromosomes to the haploid, and which constitutes the third phase of sexual reproduction. To summarize: plasmogamy brings two haploid nuclei together in one cell; karyogamy unites them into one diploid, zygote nucleus; and meiosis restores the haploid condition in the four nuclei which result from it. *In a true sexual cycle these three processes occur in a regular sequence and usually at specified points.*

Before we discuss the methods which fungi employ in accomplishing sexual reproduction, it is necessary to learn something about the organs involved. Some species produce distinguishable male and female sex organs on each thallus. Such species are **hermaphroditic** (Gr. *Hermes* = the messenger of the Gods, symbol of the male sex + *Aphrodite* = the goddess of love, symbol of the female sex). A single thallus of a hermaphroditic species can reproduce sexually by itself if it is self-compatible (see page 29 for an explanation of sexual compatibility). Other species consist of male and female thalli, some thalli producing only male sex organs and others only female sex organs. We call such species **dioecious** (NL. *di* = two + Gr. *oikos* = home; i.e., sexes segregated into two different individuals). A single thallus of a dioecious species cannot reproduce sexually by itself normally since it is either male or female.

Some species of fungi produce no differentiated sex organs, the sexual function having been delegated to somatic hyphae. Individual thalli of such fungi may or may not reproduce sexually by themselves, depending on whether they are self-compatible or self-incompatible (see page 29).

The sex organs of fungi are called **gametangia** (sing. **gametangium**; Gr. *gametes* = husband + *angeion* = vessel). These may form differentiated sex cells called gametes or may contain instead one or more gamete nuclei. We use the terms **isogametangia** and **isogametes** (Gr. *ison* = equal), respectively, to designate gametangia and gametes which are morphologically indistinguishable; we use **heterogametangia** and **heterogametes** (Gr. *heteron* = other, different) to designate male and female gametangia and gametes which are morphologically different. In the latter case, the male gametangium is called the **antheridium** (pl. **antheridia**; Gr. *antheros* = flowery + *-idion*, dimin. suffix) and the female gametangium is called the **oögonium** (pl. **oögonia**; Gr. *oön* = egg + *gonos* = offspring).

We are now ready to describe the various methods by means of which compatible nuclei are brought together in the process of

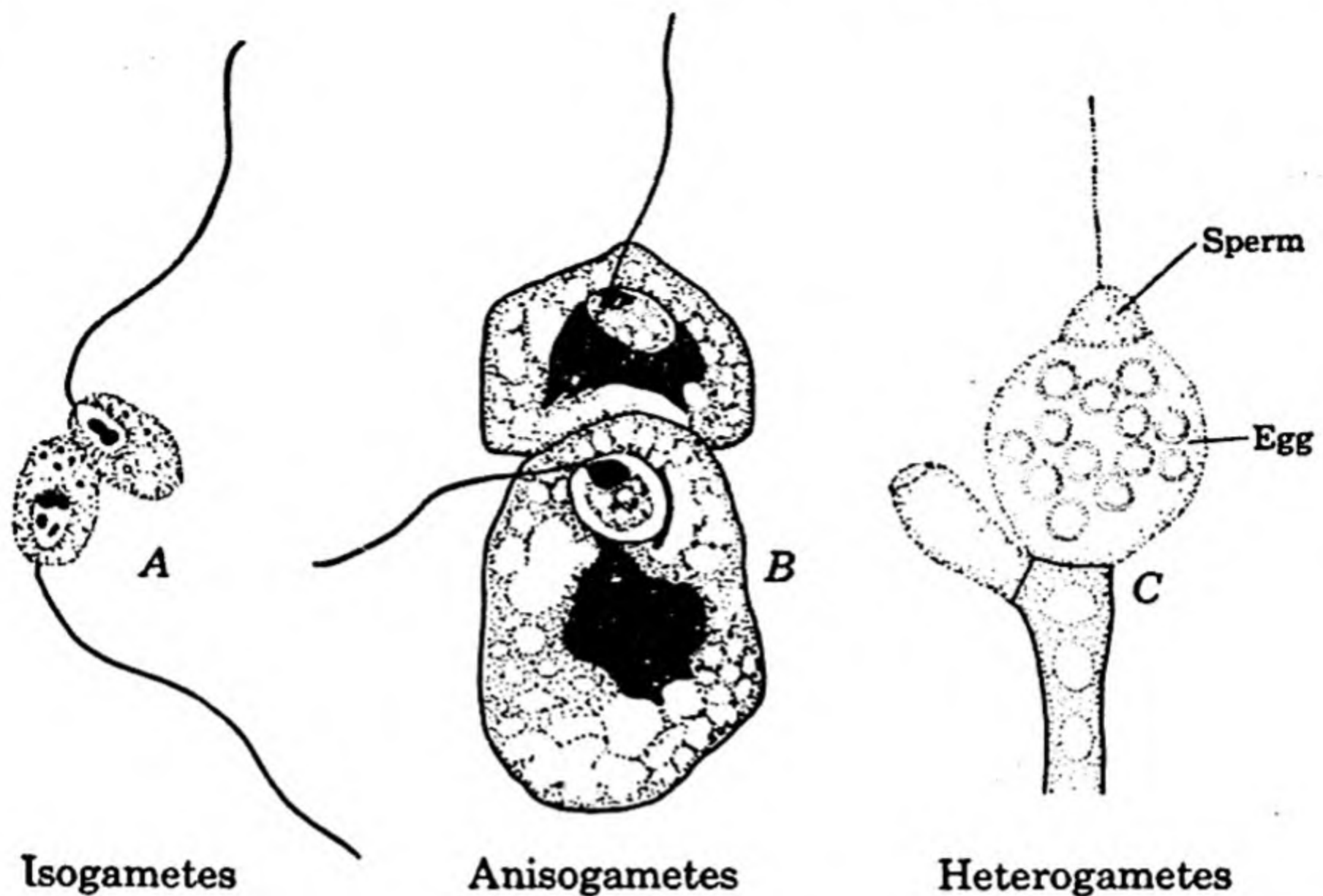


Figure 14. Sexual reproduction. Planogametic copulation. A. *Catenaria* sp. B. *Allomyces arbuscula*. C. *Monoblepharella taylori*. A, redrawn from Karling, 1934, *Mycologia*, 26:528-542; B, redrawn from Hatch, 1938, *Ann. Bot.*, n.s., 2:583-614; C, redrawn from Miss Springer, 1945, *Am. Jr. Bot.*, 32:259-269.

plasmogamy. These methods are often referred to as methods of sexual reproduction, for plasmogamy initiates this process. The most common methods are the following.

1. **Planogametic Copulation.** This involves the fusion of two naked gametes one or both of which are motile (Figure 14). Motile gametes are called **planogametes** (Gr. *planetes* = wanderer + *gametes* = husband). The most primitive fungi produce isogamous planogametes. Anisogamous planogametes (Gr. *a* = not + *isos* = equal + *gamos* = marriage), which are morphologically similar but differ in size, are produced only by one group of lower fungi belonging to the genus *Allomyces* (see page 119). In a related group (Monoblepharidales, page 123), the female gamete is non-motile whereas the male gamete is motile. The latter enters the oögonium and fertilizes the egg.

2. **Gametangial Contact.** In a large number of fungi, the gametes of the male or of both the male and the female gametangia have been reduced to undifferentiated protoplasts each consisting chiefly of a nucleus. Such gametes are never released from the gametangia

to the outside, but are transferred directly from one gametangium into the other. In this method, two gametangia of opposite sex come in contact, and one or more gamete nuclei migrate from the male to the female. In no case do the gametangia actually fuse or in any way lose their identity during the sexual act. The male nuclei, in some species, enter the female gametangium through a pore developed by the dissolution of the gametangial walls at the point of contact; in other species, an especially developed fertilization tube serves as a passage for the male nuclei (Figure 15). After the passage of the nuclei has been accomplished, the oögonium continues its development in various ways, and the antheridium eventually disintegrates.

3. Gametangial Copulation. This method is characterized by the fusion of the entire contents of two contacting gametangia. Such fusion takes place in one of two ways:

- a. Passage of the contents of one gametangium into the other through a pore developed in the gametangial walls at the point of contact. This method is particularly characteristic of some holocarpic forms in which the entire thallus acts as a gametan-

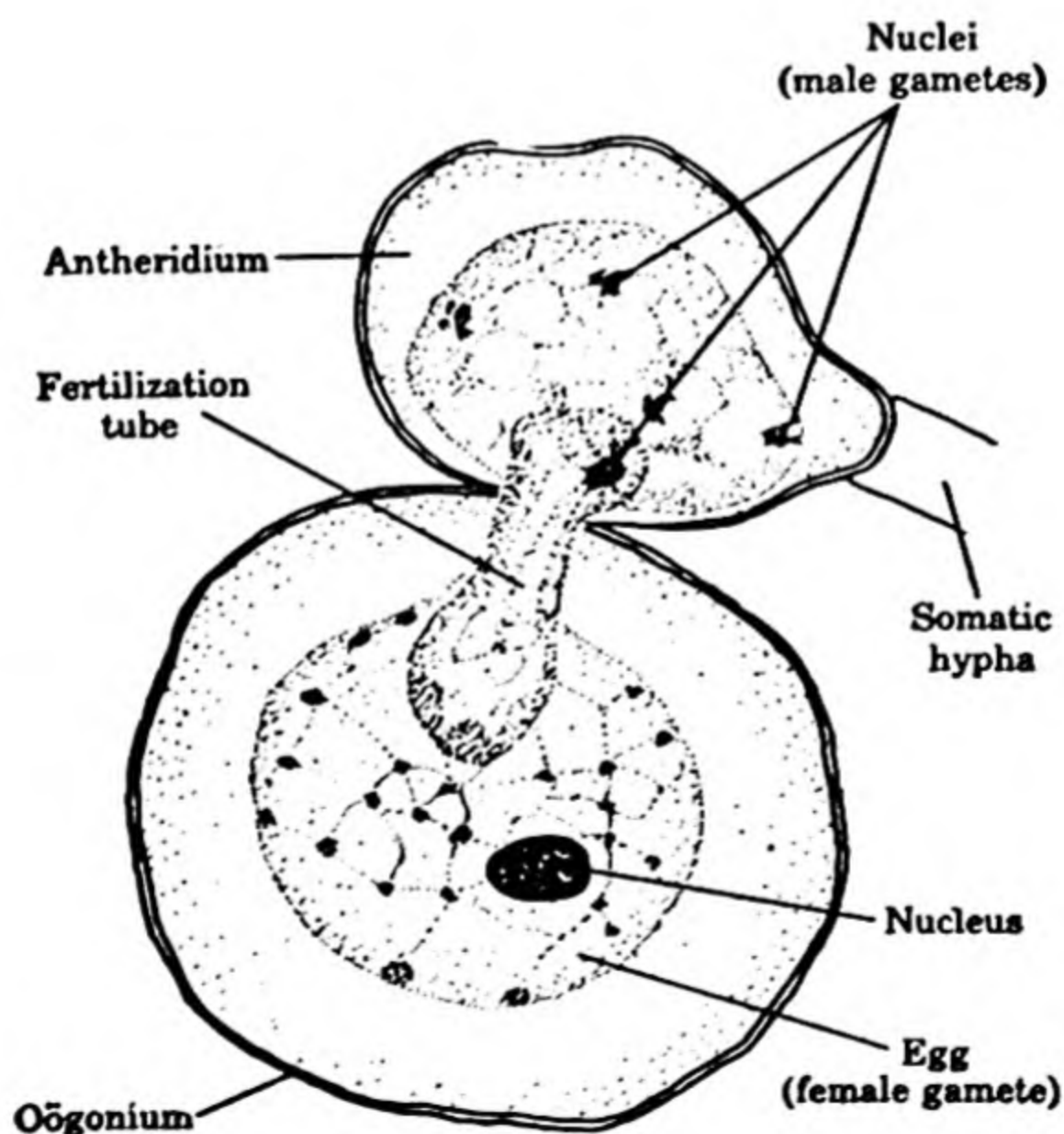


Figure 15. Sexual reproduction. Plasmogamy through gametangial contact in *Pythium aphanidermatum*. Redrawn from Edson, 1915, *Jr. Agr. Res.*, 4:279-292.

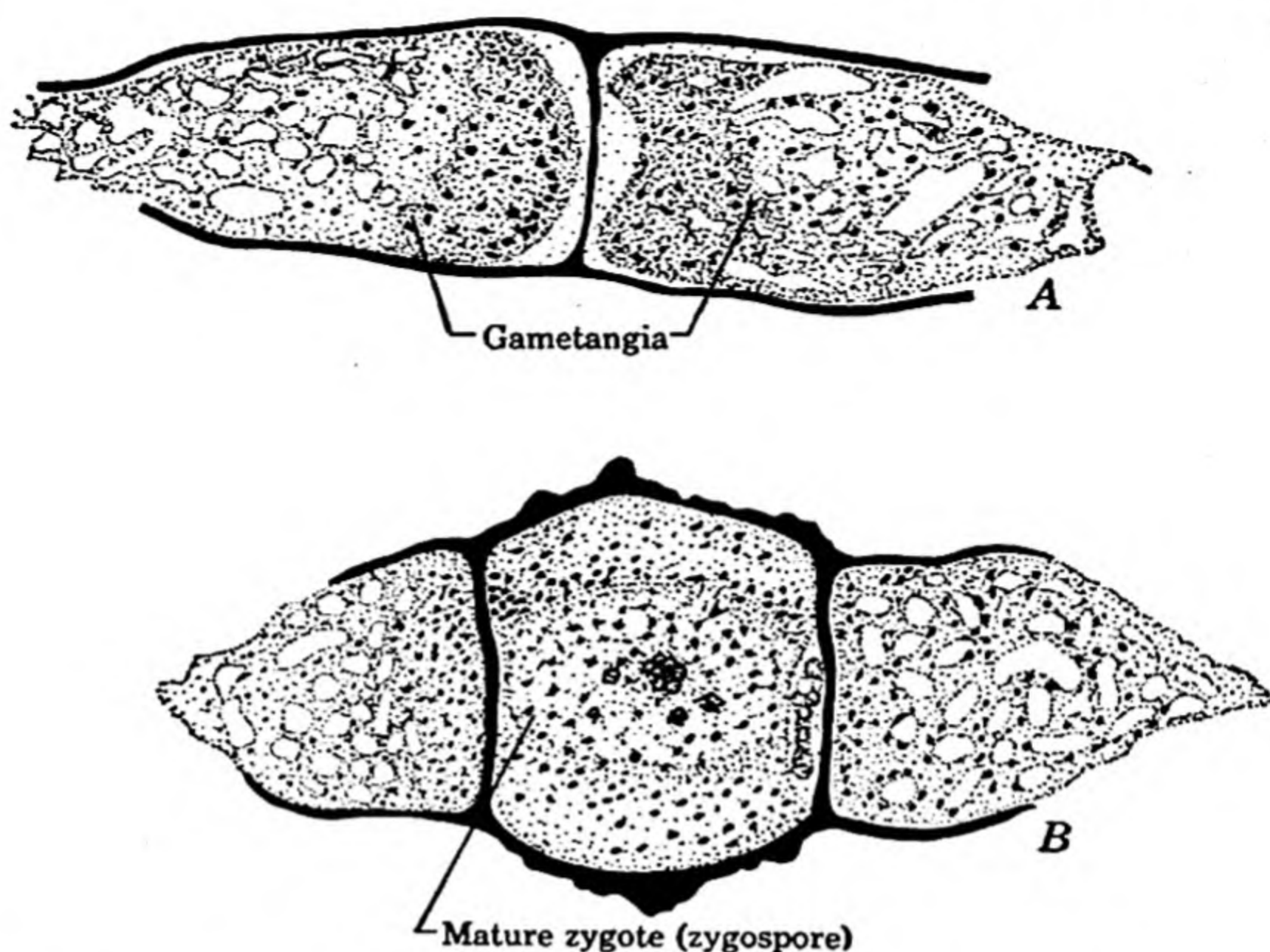


Figure 16. Sexual reproduction. Plasmogamy through gametangial copulation in *Sporodinia grandis*. Redrawn from Miss Keene, 1914, *Ann. Bot.*, 28:455–470.

gium, the male thallus attaching itself to and emptying its entire content into the female thallus (Figure 43F).

- b. Direct fusion of the two gametangial cells into one. This takes place by the dissolution of the contacting walls of the two gametangia, resulting in a common cell in which the two protoplasts mix (Figures 16, 89C, 90C).

4. **Spermatization.** Some fungi bear numerous, minute, uninucleate, spore-like, male structures termed **spermatia** (sing. **spermatium**; Gr. *spermaton* = little seed) which are produced in various ways. The spermatia are carried by insects, wind, or water, or in some other way, to the female gametangia, to special receptive hyphae, or even to somatic hyphae, to which they become attached. A pore develops at the point of contact, and the contents of the spermatium pass into the particular receptive structure which serves as the female organ (Figure 17).

5. **Somatogamy.** No sex organs whatever are produced by many of the higher fungi, somatic cells taking over the sexual function (Figure 18).

The Nuclear Cycle. As in other living organisms, so too in fungi

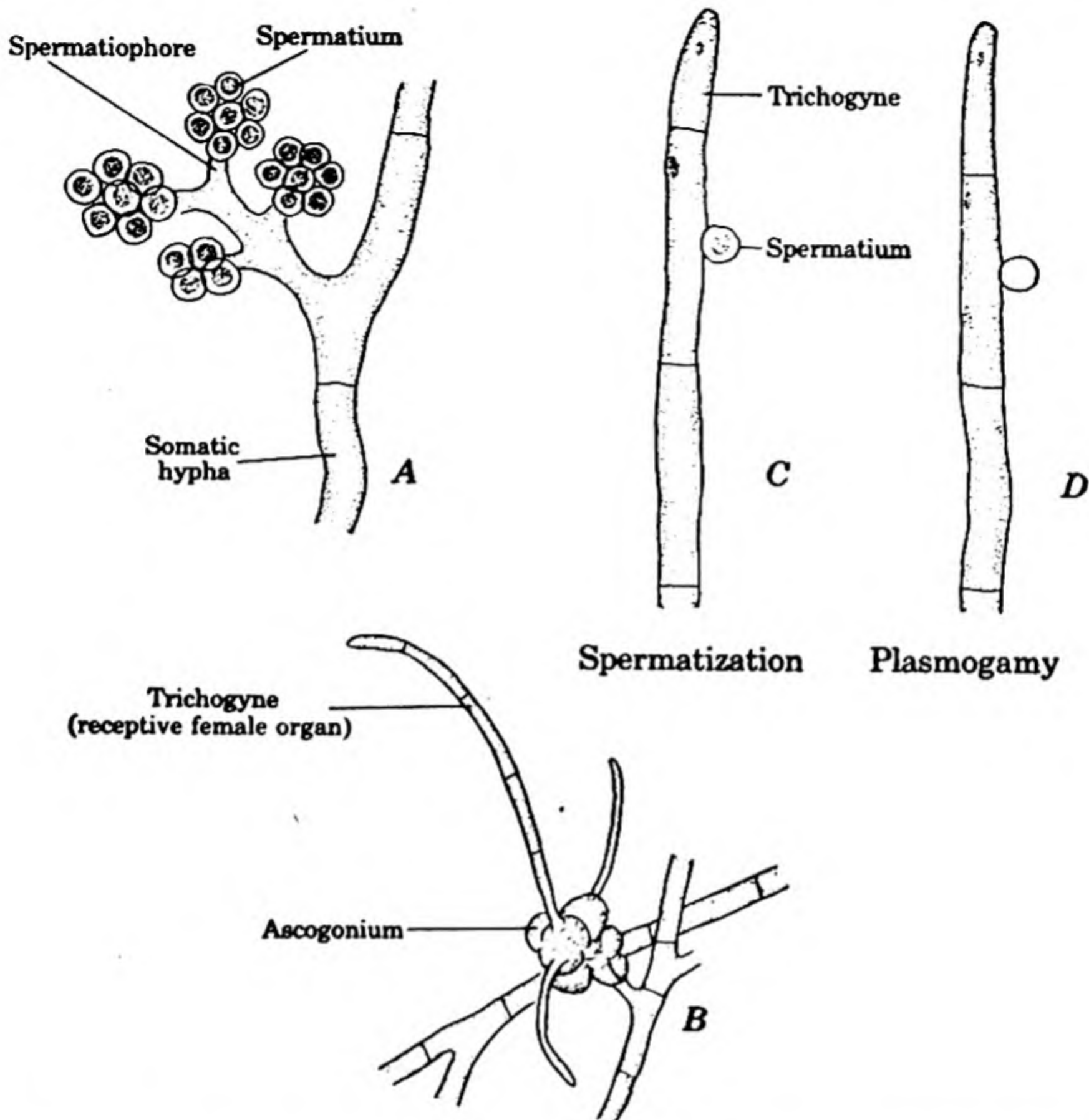


Figure 17. Sexual reproduction. Plasmogamy by means of spermatization in *Podosporea anserina*. Redrawn from Ames, 1934, *Mycologia*, 26:392-414.

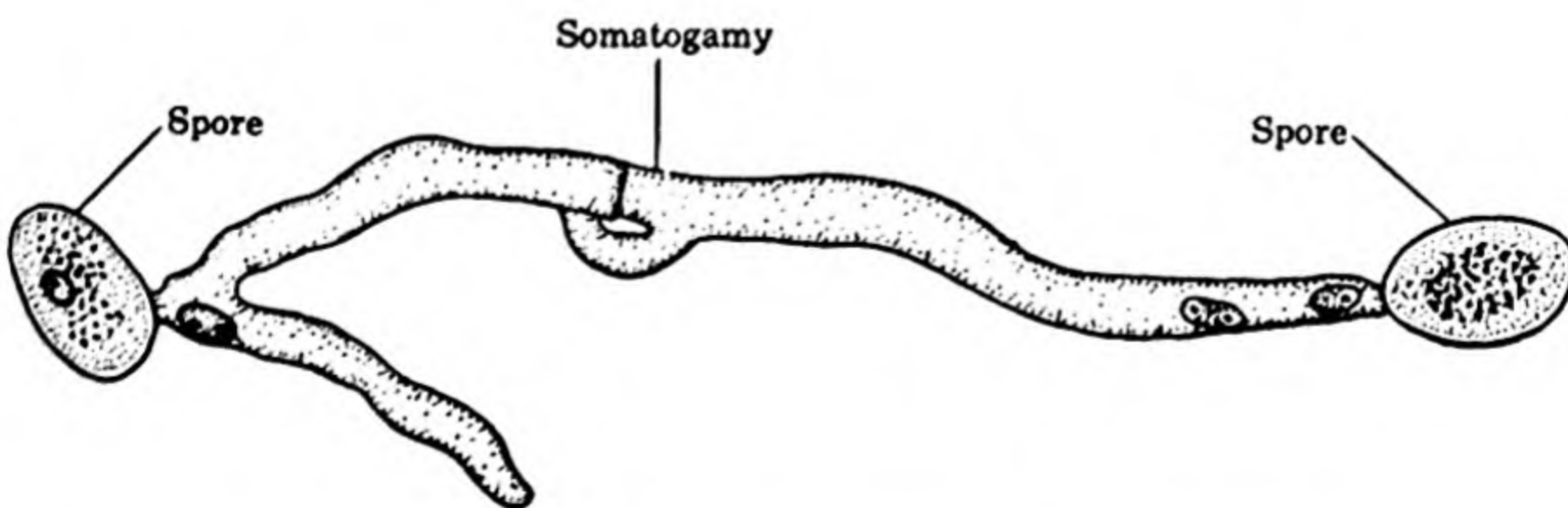


Figure 18. Sexual reproduction. Plasmogamy through somatogamy. (*Pento-phora sambuci*.) Redrawn from Lehfelddt, 1923, *Hedwigia*, 64:30-51.

there is generally a cycle of haploid and diploid structures, corresponding to the gametophyte and sporophyte in the green plants. The diploid phase begins with karyogamy and ends with meiosis. In the majority of fungi, however, there is no distinct alternation of generations. In the majority of fungi, too, the diploid phase occupies a very much smaller portion of the life cycle than does the haploid phase.

Heterokaryosis. The nuclear cycle is not always as clear cut as it may appear from the foregoing statements. Nuclei of the same or of different genotypes may coexist side by side in the same mycelium and in the same cell of a hypha. All cells do not necessarily have the same number of nuclei or the same kinds of nuclei, or the same proportion of each kind in a mixture of nuclei. This phenomenon of the existence of different kinds of nuclei in the same individual we call **heterokaryosis** (Gr. *heteros* = different + *karyon* = nut, nucleus), and the individuals which exhibit it, **heterokaryotic**.

In a heterokaryotic individual each nucleus is independent of all other nuclei, but the structure and behavior of the individual appear to be controlled by the kinds of genes it contains and the proportion of each kind, regardless of whether these are separated in different nuclei or not.

Heterokaryosis may originate in a fungal thallus in four ways:

1. By the germination of a heterokaryotic spore, which will give rise to a heterokaryotic soma.
2. By the introduction of genetically different nuclei into a **homokaryon** (Gr. *homo* = same + *karyon* = nut, nucleus), a soma in which all nuclei are similar.
3. By mutation in a multinucleate, homokaryotic structure and the subsequent survival, multiplication, and spread of mutant nuclei among the wild-type nuclei.
4. By fusion of some nuclei in a haploid homokaryon and the subsequent survival, multiplication, and spread of the diploid nuclei among the haploid.¹

Thus in some fungi it is possible to have not only different kinds of haploid nuclei in the same soma, but also a mixture of haploid and diploid nuclei. Whether this last situation is widespread in nature we do not know. Certainly, in most fungal individuals the haploid and diploid phases of the life cycle are clearly distinguishable.

¹ Although, strictly speaking, the result would be a heterokaryon no new genes are introduced in such a situation.

Sexual Compatibility. We have already discussed the various methods by means of which two nuclei are brought together in the same cell as a preliminary condition to nuclear fusion. It is now necessary to say something about sexual compatibility in the fungi.

To discuss so complex a topic in an introductory textbook is a difficult task. You should understand at the very beginning that what follows constitutes only the barest outline and approaches an oversimplification of the subject. Although compatibility is certainly closely related to sex because, in a way, it governs sexual reproduction, it should not be confused with sex. There are, for example, a great many fungi which produce clearly distinguishable male and female sex organs on the same thallus but in which, nevertheless, single individuals¹ are sexually self-sterile because their male organs are incompatible with their female organs and no plasmogamy can take place.

On the basis of sex, most fungi may be classified into three categories:

- A. *Hermaphroditic*, in which each thallus bears both male and female organs.
- B. *Dioecious*,² in which some thalli bear only male and some thalli bear only female organs.
- C. *Sexually undifferentiated*, in which sexually functional structures are produced which are morphologically indistinguishable as male or female.

Fungi in the above sex categories belong to one or another of the following three groups on the basis of compatibility:

1. *Homothallic Fungi*. Those in which every thallus is sexually self-fertile and can, therefore, reproduce sexually by itself without the aid of another thallus. Obviously, no dioecious fungus can be homothallic.

2. *Heterothallic Fungi*. Those in which every thallus is sexually self-sterile and requires the aid of another compatible thallus of a different mating type for sexual reproduction.

Heterothallic fungi belong to one or the other of the following two general groups:

- a. *Bipolar heterothallic*. Fungi in this category consist of two groups (mating types) of individuals which differ in their genetic make-up for the compatibility factor. Each nucleus of

¹ An individual is a thallus which has originated from a single spore.

² Some mycologists prefer to designate these fungi as sexually dimorphic.

one mating type carries the gene **A**, and each nucleus of the other mating type carries the gene **a**. Only thalli whose nuclei carry opposite genes of this Mendelian pair **Aa** are compatible.

b. Tetrapolar heterothallic. Fungi in this category consist of four basic groups (mating types) of individuals. Compatibility here is governed by two pairs of factors, **Aa** and **Bb**, located on different chromosomes. Only thalli whose nuclei carry opposite genes of both Mendelian pairs **Aa** and **Bb** are compatible, the resulting zygote having the genotype **AaBb**. In tetrapolar fungi, the situation becomes infinitely complicated by the existence of many alternate factors for each gene **A**, **a**, **B**, **b**.

3. Secondarily Homothallic Fungi. In some bipolar heterothallic fungi an interesting mechanism operates during spore formation whereby two nuclei of opposite mating type are incorporated regularly in each spore. Each spore, therefore, upon germination gives rise to a thallus which contains both **A** and **a** nuclei and consequently behaves as though it were homothallic. This condition has been called secondary homothallism.

What we have said up to now refers chiefly to the morphological and genetic control of the sexual process. But there is another phase which we must not overlook. It is the physiological or chemical aspect of the problem. Is the meeting and fusion of two genetically compatible organs or gametes entirely left to chance in the fungi, or is there some mechanism which increases the probability of such a tryst? Our information on this subject is far from complete, but we do know that in many fungi there are very definite physiological mechanisms superimposed on the genetic which govern sexuality. The best known is the secretion of sexual hormones which control the sexual process step by step from the initiation of the sexually active organs or gametes to karyogamy. We shall discuss some of these mechanisms in connection with individual groups of fungi in which they are known to occur.

Parasexuality. Some fungi do not go through a true sexual cycle as we have defined it, but derive many of the benefits of sexuality through parasexuality (Gr. *para* = beside + *sex*). This is a process in which plasmogamy, karyogamy, and haploidization take place, *but not at specified points in the thallus or the life cycle*. We shall discuss the parasexual cycle in more detail in connection with the Deuteromycetes in Chapter 18. The Deuteromycetes are fungi in which sexual reproduction does not take place and in which the parasexual cycle is of paramount importance. Nevertheless, the

sexual and parasexual cycles are not mutually exclusive. Some fungi which reproduce sexually also exhibit parasexuality.

A number of excellent review papers on sexual and parasexual mechanisms in the fungi are listed at the end of this chapter.

Classification. The classification of the fungi presents innumerable difficulties with which, however, you as a beginning student need not be confronted. At the same time, you must understand that all is not settled in mycology and that differences of opinion on classification are so numerous and often so great among mycologists that you will find what appear to be serious discrepancies in the "standard" literature of the science. Such differences in classification are due to differences of interpretation of our fragmentary data on the structure, development, and physiology of the fungi, and will continue to exist until the gaps in our knowledge are filled.

Taxonomy has a dual purpose: first, to name organisms according to some internationally accepted system so that, with the least possible amount of confusion, mycologists may communicate to each other their findings concerning a certain fungus; second, to indicate, so far as we know them, the relationships of fungi to each other and to other living organisms. As our knowledge increases, our classification is bound to change. Even the names of organisms do not always remain stable because, as we learn new facts about them, it often becomes necessary to alter our concept of their relationships, which in turn demands reclassification and a change of name.

The groupings or categories used in the classification of the fungi are as follows:

Kingdom
Division
Class
Order
Family
Genus
Species

The kingdom is the largest of the categories and includes many divisions; each division may include many classes, and so on down to the **species** (sing. and pl. **species**; L. *species* = kind), which is the unit of classification. Each of these categories may be divided into sub-groups, as sub-division, sub-class, sub-order, if necessary. Species are sometimes broken down into varieties, biological strains, and physiological or cultural races, about which more will be said in later chapters.

In accordance with the recommendations of the committee on International Rules of Botanical Nomenclature, the names of the divisions of fungi should end in *-mycota*, of sub-divisions in *-mycotina*, of classes in *-mycetes*, and of sub-classes in *-mycetidae*. Names of orders end in *-ales*, and of families in *-aceae*. Genera (sing. genus; L. *genus* = race) and species have no standard endings.

The name of an organism is a **binomial** (L. *bi* = two + *nomen* = name), i.e., it is composed of two words. The first is a noun designating the genus in which the organism has been classified, and the second is often an adjective, describing the noun, which denotes the species. The genus name is always capitalized. The modern tendency is not to capitalize the species name regardless of its derivation. This policy will be followed throughout this book. Binomials are frequently descriptive of the organisms and are usually derived from Greek or Latin, since these languages are internationally known by scholars. For example, *Schizosaccharomyces octosporus* is the name of a yeast which divides by fission and which produces eight spores. *Schizosaccharomyces* means fission-sugar-fungus, i.e., a yeast which divides by fission (Gr. *schizo* = I tear + *saccharon* = sugar + *mykes* = fungus); *octosporus* means eight-spored (Gr. *okto* = eight + *sporos* = seed, spore).

Binomials when written should always be underlined, and when printed italicized. The name or the abbreviated name of the scientist who first described the species sometimes follows the binomial, thus: *Schizosaccharomyces octosporus* Beyerinck. Some binomials are followed by two names, the first of which is in parentheses, thus: *Aplanes treleaseanus* (Humphrey) Coker. The name in parentheses is that of the person who first described the species, but used a different name from the one currently recognized. The name which follows the parentheses is that of the person who is responsible for the binomial as it now stands. Accordingly, Humphrey described *Aplanes treleaseanus* (Humphrey) Coker in 1893, but named it *Achlya treleaseanus* Humphrey. In 1923 Coker decided that this organism should be placed in the genus *Aplanes* and consequently changed the name to *Aplanes treleaseanus* (Humphrey) Coker. The reason for such author citations is to aid the taxonomist in finding the original and subsequent descriptions of an organism when necessary, and to avoid confusion when different authors use the same binomial accidentally to name different species. To aid the taxonomist further, the year in which an organism was described is sometimes written after the author's name following the binomial.

To continue with the classification of our original example, the

species *octosporus* is one of several in the genus *Schizosaccharomyces*. The latter, together with other genera, belongs to the family Saccharomycetaceae, which includes most of the yeasts. This family, together with others, belongs to the order Endomycetales. This order, in turn, with two other orders we place in the sub-class Hemiascomycetidae, which is one of three sub-classes of the class Ascomycetes. The class Ascomycetes is one of eight classes which constitute the sub-division Eumycotina. The Eumycotina and the Myxomycotina are the two sub-divisions of the division Mycota—the fungi. Most mycologists continue to place the Mycota in the kingdom Plantae. This classification may be represented as follows:

Kingdom: Plantae
Division: Mycota
Sub-division: Eumycotina
Class: Ascomycetes
Sub-class: Hemiascomycetidae
Order: Endomycetales
Family: Saccharomycetaceae
Genus: *Schizosaccharomyces*
Species: *octosporus*

There is a tendency for the beginning student to regard these various taxonomic categories as concrete and stable, and more or less sacred. Such an attitude will lead to disappointment with the first attempt to identify an unknown organism. You should understand, above all, that living organisms are constantly evolving, and that any attempt to pigeonhole them into a system of classification is bound to meet with difficulties. All systems of classification are nothing more than the attempts of man to organize his knowledge, and are strictly man-made. Even when our knowledge of fungi becomes much greater than it is at present, any attempt to draw hard and fast lines between taxonomic categories will be futile, because the categories themselves are only human concepts and intermediate forms are bound to exist and to arise by hybridization and mutation. As a matter of fact, the more we study living organisms, the more we are inclined to agree with Hochreutiner (1929, pp. 151–152) that “in nature there are no families, no genera, no species . . . ; there are only individuals more or less resembling one another.” If you keep these facts in mind, you will be more tolerant toward taxonomic idiosyncrasies and will find it easier to control your temper when the specimen at hand does not quite fit the key which at the moment you are using as an aid to identification.

Indeed, at the very outset we are confronted with a difficult de-

cision concerning the proper place of fungi in the living world. In some of their characteristics fungi resemble plants; in others they resemble animals. Some mycologists have concluded that the fungi have evolved from the algae by loss of chlorophyll. If that is true, the fungi are plants and are properly placed in the plant kingdom. Mycologists of another school, however, believe that the fungi had a common ancestry with the protozoa but split off at a very early stage of organic evolution. If this theory is correct, the fungi are neither plants nor animals: they are fungi!

The dilemma is an old one. Ever since man began studying living organisms he has always thought of them as being either plants or animals. Linnaeus, who was the father of systematic biology, placed the fungi in the plant kingdom and there they have traditionally remained to the present time. Nevertheless, as the study of microscopic structure progressed, it became more and more evident that the border line between the plant and animal kingdoms is not always clear and that many groups of organisms, like the fungi, straddle this man-made fence. In an attempt to solve the problem, the German biologist Ernst Haeckel proposed in 1866 that a third kingdom, the **Protista** (Gr. *protiston* = the very first), be recognized to include all organisms which did not clearly belong in either the plant or the animal kingdom. This idea has been expanded by several biologists who have proposed four kingdoms of living organisms. The most ambitious of these systems is Copeland's (1956). But, in the words of Cronquist (1960), "... although a four-kingdom system has some advantages, it still does not avoid the necessity to draw arbitrary lines, and in at least some respects it is less natural than a two-kingdom system."¹ This is the view we shall adopt in this book. Certainly we cannot settle here a question over which biologists have argued for a century, but the problem is one to which every student should give some thought. You will find Copeland's book challenging. You should also read Martin's (1955) stimulating article, "Are Fungi Plants?"

Modern systematists divide the plant kingdom into many divisions and place the fungi, including the true slime molds, in the division Mycota, or Fungi. Two orders to which we shall devote some space, the Acrasiales and the Labyrinthulales, are of such uncertain affinities that we shall not attempt to link them with any division in the plant or animal kingdom. Perhaps they should constitute separate divisions until we learn more about their relationships.

¹ Quoted by permission from *Botanical Review*.

Order Acrasiales. These are the cellular slime molds. The somatic structure of the Acrasiales is a simple amoeboid cell. No flagellated cells are produced. Aggregation of amoebae into a communal **pseudoplasmodium** (Gr. *pseudo* = false + *plasmodium* = the soma of the Myxomycetes) precedes sporulation. The spores are borne on various types of fructifications but are never enclosed in a common membrane. Sexual reproduction is by engulfment of one amoeba by another, and a subsequent fusion of the nuclei.

Order Labyrinthulales. This order includes marine or fresh-water parasites or saprobes whose somatic structure is a simple oval or spindle-shaped cell. The cells secrete mucous filaments which unite to form a fine network on which the cells glide. Sexual reproduction is unknown.

Division Mycota. These are the fungi. The soma varies from a microscopic unicell to an extensive mycelium. True nuclei with nuclear membranes and nucleoli are present. The cell walls contain chitin or cellulose, or a mixture of both, and other complex polysaccharides. Reproduction is typically both asexual and sexual. The propagative units are the spores. We recognize two subdivisions: the **Myxomycotina** or true slime molds, and the **Eumycotina**, or true fungi.

1. **Sub-division Myxomycotina.** This sub-division contains the single class Myxomycetes. The chief characteristic of the slime molds is the absence of definite cell walls from their amoeboid, animal-like bodies. The somatic structure of the Myxomycetes is a free-living **plasmodium** (pl. **plasmodia**; Gr. *plasma* = a molded object, a being), a multinucleate mass of protoplasm devoid of definite cell walls. The entire plasmodium, whose nuclei are characteristically diploid, is consumed in the formation of fructifications which bear spores resulting from meiosis. The portion of the fructification which bears the spores is surrounded—except in three species—by a **peridium** (pl. **peridia**; Gr. *peridion* = a small leather pouch) which, however, may disappear at a very early developmental stage. Flagellated cells are characteristically produced.

2. **Sub-division Eumycotina.** These are the true fungi. Organisms included in this sub-division are, with few exceptions, provided with cell walls and are typically filamentous, although some unicellular types occur. They reproduce both sexually and asexually. The Eumycotina are subdivided into eight classes, as follows:

a. **Class Chytridiomycetes.** Fungi, with a variety of thalli, whose motile cells possess a single posterior whiplash flagellum.

b. Class Hyphochytridiomycetes. A very small group of aquatic fungi whose motile cells possess a single anterior tinsel flagellum.

c. Class Oömycetes. Fungi with a usually well-developed coenocytic mycelium, whose motile cells possess two oppositely directed flagella, one whiplash, the other tinsel. Sexual reproduction resulting in the formation of a resting spore formed from the fertilized egg.

d. Class Plasmodiophoromycetes. Parasitic fungi with non-cellular (devoid of cell walls), multinucleate thalli living in the cells of their hosts. Resting spores produced in masses, but not in distinct fruiting bodies. Motile cells possess two anterior whiplash flagella.

e. Class Zygomycetes. Saprobiic or parasitic fungi with a well-developed coenocytic or septate mycelium. Sexual reproduction resulting in the formation of a resting spore formed by the fusion of two usually equal gametangia. No motile cells produced.

f. Class Trichomycetes. Fungi with a simple or branched filamentous coenocytic thallus, attached to the digestive tract or the external cuticle of living arthropods. Asexual reproduction by a variety of spores. Sexual reproduction where known as in the Zygomycetes.

g. Class Ascomycetes. Fungi which form spores, resulting from karyogamy and meiosis, inside special sac-like structures called **asci** (sing. *ascus*; Gr. *askos* = sac).

h. Class Basidiomycetes. Fungi which form spores, resulting from karyogamy and meiosis, on the surface of special structures called **basidia** (sing. *basidium*; Gr. *basidion* = small base).

i. Form-class Deuteromycetes. In addition to the eight classes listed above, we recognize a ninth group (form-class) in which we place fungi which, in their general structure and asexual reproduction, resemble the Ascomycetes or Basidiomycetes, but in which sexual stages have not been discovered. This form-class is also known as Fungi Imperfecti.

SIMPLIFIED KEY TO THE CLASSES OF FUNGI (DIVISION MYCOTA) AND TO FUNGUS-LIKE ORGANISMS DEVOID OF CHLOROPHYLL

- | | |
|---|------------------------------|
| A. Somatic phase consisting entirely of simple, uninucleate amoebae | B, BB |
| AA. Somatic phase not of simple, uninucleate amoebae | C, CC |
| B. Amoebae aggregating into a pseudoplasmodium | Order <i>Acrasiales</i> |
| BB. Amoebae sliding on a network of slimy filaments | Order <i>Labyrinthulales</i> |

- C. Nuclei devoid of a nucleolus and of a nuclear membrane; somatic phase of minute single cells or filaments rarely exceeding $2\ \mu$ in diameter
- CC. Nuclei with one or more nucleoli and provided with a nuclear membrane; somatic phase filamentous, unicellular (the filaments or cells usually over $2\ \mu$ in diameter), or plasmodial
- D. Somatic phase a free-living plasmodium
- DD. Somatic phase not a free-living plasmodium
- E. Flagellated cells characteristically produced
- EE. Flagellated cells lacking or rarely produced
- F. Motile cells uniflagellate
- FF. Motile cells biflagellate
- G. Flagellum posterior, whiplash
- GG. Flagellum anterior, tinsel
- H. Flagella of unequal size, both whiplash
- HH. Flagella nearly equal, one whiplash, the other tinsel
- I. Hyphae aseptate, or if septate then sexual reproduction resulting in the formation of a resting spore
- II. Hyphae septate; sexual reproduction not resulting in the formation of a resting spore
- J. Soma filamentous, attached to digestive tract or external cuticle of living arthropods; mycelium not immersed in host tissues
- JJ. Mainly saprobic; if attacking living arthropods, then mycelium developing in host tissues before sporulating
- K. Sexual reproduction resulting in the formation of ascospores or basidiospores
- Class *Schizomycetes*
(not discussed in this book)
- Division *Mycota* (D, DD)
- Sub-division *Myxomycotina*
Class *Myxomycetes*
- Sub-division *Eumycotina* (E, EE)
- F, FF
- I, II
G, GG
H, HH
Class *Chytridiomycetes*
Class *Hyphochytridiomycetes*
- Class *Plasmodiophoromycetes*
- Class *Oömycetes*
- J, JJ
- K, KK
- Class *Trichomycetes*
- Class *Zygomycetes*
- L, LL

KK. Sexual reproduction lacking; a parasexual cycle may be present

Form-class *Deuteromycetes*

L. Spores resulting from karyogamy and meiosis borne in asci

Class *Ascomycetes*

LL. Spores resulting from karyogamy and meiosis borne on basidia

Class *Basidiomycetes*

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PART II ORGANISMS
OF UNCERTAIN
AFFINITY

2 order ACRASIALES the cellular slime molds

General Characteristics. The Acrasiales are a group of organisms we seldom see in nature because of their delicate, inconspicuous, and ephemeral fructifications and their microscopic somatic phase.

The unit of structure of the Acrasiales is a uninucleate, naked, haploid amoeba which feeds on bacteria. No flagellated cells are produced. What distinguishes the cellular slime molds from most other organisms discussed in this book, however, is the aggregation of these amoebae to form a pseudoplasmodium in which the component amoebae do not fuse, but retain their individuality, yet cooperate as members of a well-organized community until sporulation occurs. Because of this phase of the life cycle, the Acrasiales have often been called communal slime molds.

The fruiting bodies of the Acrasiales we call **sorocarps** (Gr. *soros* = heap + *karpos* = fruit). They vary from almost microscopic papillae in the genus *Guttulinopsis* to the delicate, but relatively large, many-branched fructifications of *Polysphondylium*, which may reach a length of a centimeter or more. The sorocarp of some species is simple and bears a single head of spores at its tip. In other species it is variously branched and bears a head of spores at the tip of each branch (Figure 19).

Occurrence, Isolation, and Importance to Man. The study of the cellular slime molds began in 1869 when Oskar Brefeld, a German mycologist, discovered and described *Dictyostelium mucoroides*. By 1902 enough information had accumulated concerning these organisms to warrant a monograph by E. W. Olive which remained the standard reference work on the Acrasiales for over 30 years. For a long time, however, biologists considered the Acrasiales to be no more than a curious, rare group of organisms. Most biologists had

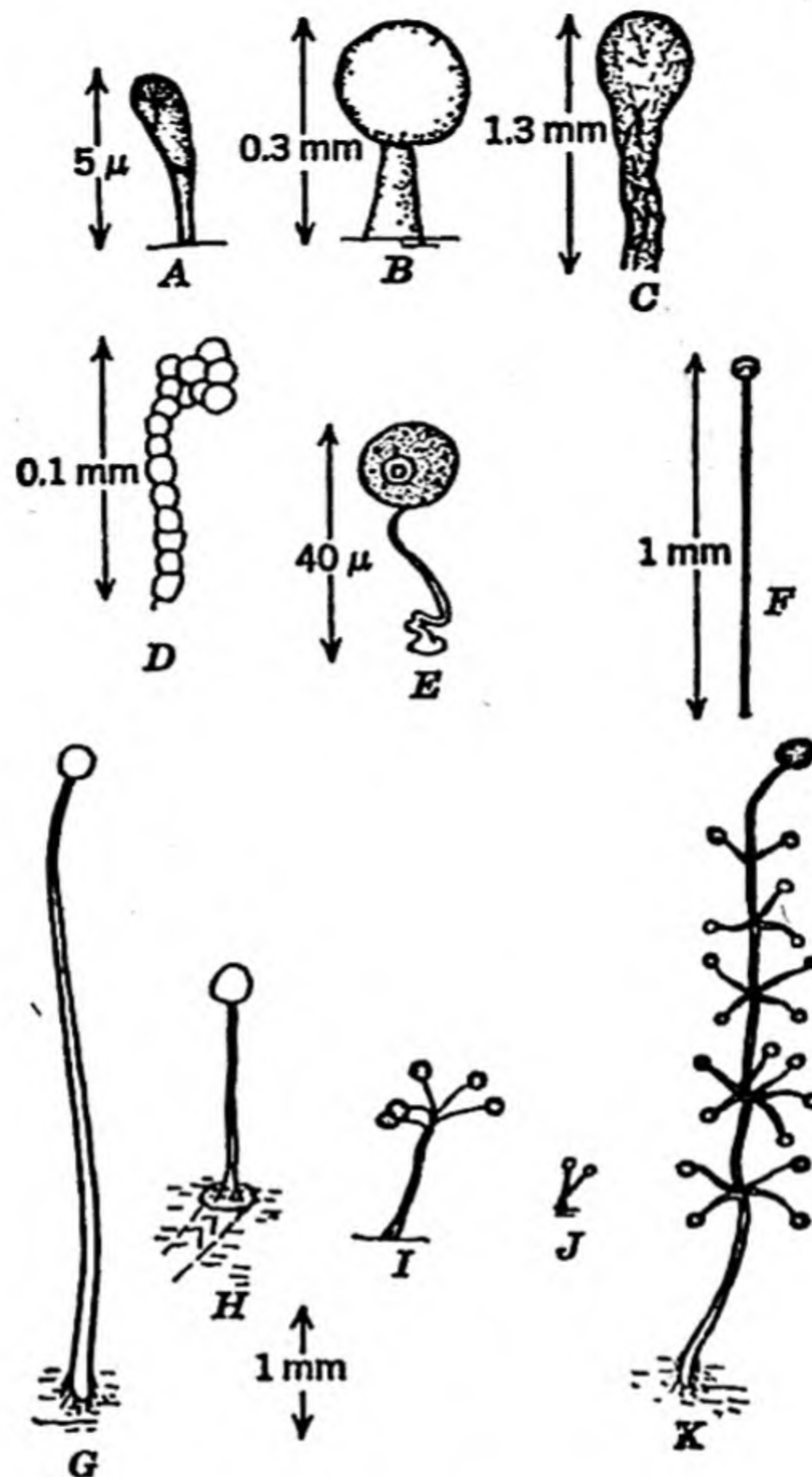


Figure 19. Sorocarps of some Acrasiales. A. *Sappinia*. B. *Guttulina*. C. *Guttulinopsis*. D. *Acrasis*. E. *Protostelium*. F. *Acytostelium*. G–J. *Dictyostelium*. K. *Polysphondylium*. A–C, drawn from photographs in Raper, 1960, *Proc. Am. Phil. Soc.*, 104:579–604; D–E, redrawn from Olive and Stoianovitch, 1960, *Bull. Torrey Bot. Club*, 87:1–20; F, after Raper, 1958, *Jr. Gen. Microbiol.*, 18:16–32; G–H, J–K, redrawn from Raper, 1951, *Quart. Rev. Biol.*, 26:169–190; I, drawn from photograph in Raper, 1956, *Jr. Gen. Microbiol.*, 14:716–732.

never seen them, and they were seldom mentioned in any but the most complete reference works. Krzemieniewska (1927) reported that she had found *Dictyostelium mucoroides*, the most common of the Acrasiales, to occur widely in Polish soils, and a few other workers had also isolated this and other species from soils, but it was not until the middle 1930's that the study of the Acrasiales received

its greatest stimulus. In 1932, Raper and Thom of the U. S. Department of Agriculture published a paper in which they pointed out that the Acrasiales were not nearly so rare as biologists believed them to be. Three years later Professor K. B. Raper discovered *Dictyostelium discoideum* (Raper, 1935) and began a series of researches which literally put the Acrasiales on the biological map. From 1932 to 1959, the year in which Dr. John T. Bonner's book, *The Cellular Slime Molds*, brought together the existing literature in an excellent discussion of all that was known concerning the Acrasiales up to that time, no fewer than 100 research papers dealing with this group were published, four times as many as in all the years before. Of these, over half appeared in the last decade covered by Bonner's book (1950-1959).

The Acrasiales are easy to isolate. All you need to do is prepare hay infusion or glucose peptone agar, pour it in sterile Petri dishes, allow it to solidify, and sprinkle some soil particles on it. Cultivated soils seem to be richer in Acrasiales, but woodland soils with leaf mold also yield good cultures. A more refined but not much more complicated technique is described by Raper (1951). None of the Acrasiales has been grown in pure culture on a chemically defined medium. Experimental work is carried on in two-membered culture with the bacterium *Escherichia coli* or with *Aerobacter aerogenes*.

Being as abundant and widespread as they are, and feeding upon bacteria, the Acrasiales undoubtedly have a role to play in the economy of nature, but their direct importance to man is confined to their usefulness in the laboratory as experimental tools, particularly in studies on morphogenesis.

Life Cycle. Most of our information concerning the life cycle of the Acrasiales is based on studies of *Dictyostelium discoideum*. The general life cycle (Figure 20) is thought to be as follows. The spores germinate and each releases one naked amoeba. The amoebae multiply by mitosis and produce a large haploid population. Centers of aggregation are then set up toward which amoebae stream and mass into a pseudoplasmodium which behaves as a unit, but in which the amoebae retain their individuality at all times. After a period of migration (in *Dictyostelium discoideum* and a few other species) the pseudoplasmodium changes into a sorocarp which bears the spores. Controversial points in the life cycle and some of the details which make these organisms of particular interest in the study of morphogenesis are briefly outlined below. Much of this material is discussed in detail in Dr. Bonner's book.

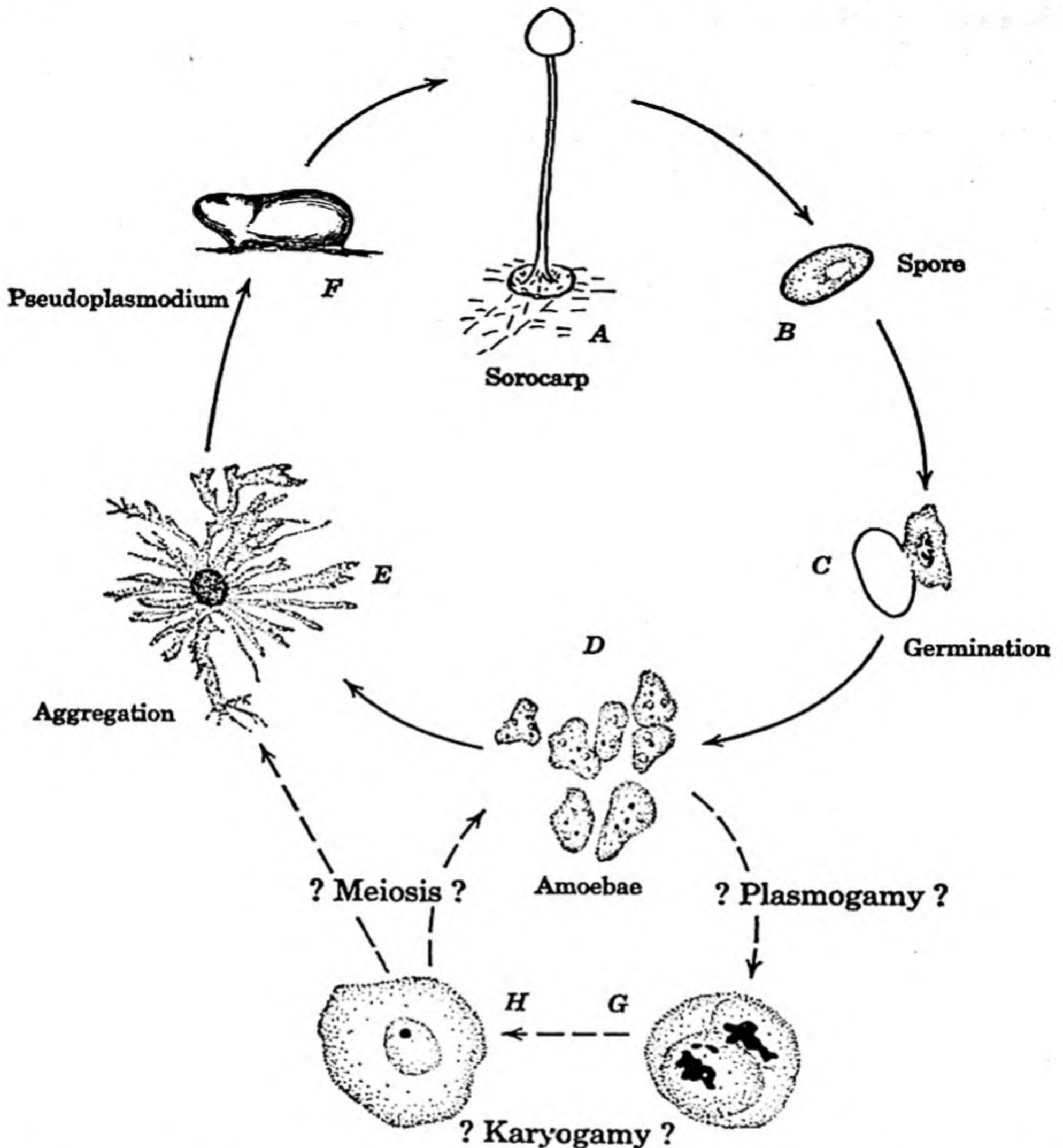


Figure 20. Probable life cycle of *Dictyostelium discoideum*. A, redrawn from Raper, 1951, *Quart. Rev. Biol.*, 26:169-190; E, drawn from photograph in Raper, *ibid.*; F, drawn from photograph in Raper, 1935, *Jr. Agr. Res.*, 50:135-147; G, drawn from photomicrograph in Wilson, 1953, *Am. Jr. Bot.*, 40:714-718.

Spores, Amoebae, and Microcysts. The spores of the Acrasiales are produced on various types of fruiting bodies. In the majority of species, the spores are ovoid or globose, with definite, smooth cell walls containing cellulose. In a few species the spores are naked, without cell walls, and are then called **pseudospores** (Gr. *pseudo* =

false + *sporos* = seed, spore). At 22° C., in the dark, spore germination begins about 1½ hours after the spores are planted on nutrient agar. After about 4 hours 98 per cent of the spores have germinated (Russell and Bonner, 1960). When a spore germinates, a single uninucleate haploid amoeba issues from the spore wall. It soon begins to feed on bacteria, ingesting them, forming food vacuoles, and digesting them. Under unfavorable conditions the amoebae encyst (Blaskovics and Raper, 1957). An encysted amoeba, termed a **microcyst** (Gr. *mikros* = small + *kystis* = bladder), is one which has rounded up and enveloped itself by a delicate but rigid cellulose wall. When favorable conditions return, a microcyst germinates. A pore is formed in the wall through which the protoplast escapes as an amoeba.

Asexual Reproduction. As the amoebae feed and grow, they divide, their nuclei undergoing mitosis followed by a pinching of the cytoplasm, which eventually results in the separation of two uninucleate amoebae from each parent cell. Divisions take place rapidly and usually continue as long as bacteria are present and conditions are favorable. By transferring amoebae frequently to fresh media in which bacteria abound, the somatic phase of these organisms may be perpetuated indefinitely under laboratory conditions.

Sexual Reproduction. The matter of the occurrence of sexual reproduction in the Acrasiales is still somewhat controversial at this time. In 1920 Skupienski wrote that he saw amoebae fusing in pairs to form zygotes, but no one gave much credence to his observations. In 1953, Dr. Charles Wilson of McGill University presented some strong evidence for sexual reproduction in *Dictyostelium discoideum*. He stated that plasmogamy takes place between pairs of amoebae at the outer fringes of a population, and that the zygotes thus formed migrate toward the center of the population, attracting other zygotes and setting up centers of aggregation. Soon after the first zygotes have formed a center of aggregation, meiosis takes place, producing a large number of haploid cells which join to form a pseudoplasmodium. Wilson stated that, when plasmogamy occurs, one amoeba completely engulfs the other. The two protoplasts soon fuse, and the two nuclei, now in the same matrix, unite and form the diploid nucleus of the zygote. Wilson agreed with Skupienski in stating that the zygotes are much larger than the haploid amoebae and may be distinguished under the microscope by their size.

Wilson and Ross (1957), continuing this line of research, supported Wilson's previous conclusions. Later Ross (1960) discussed his studies of haploid and diploid strains of *Dictyostelium discoideum*

and stated that, whereas the diploid strains with fourteen chromosomes showed no evidence of sexuality, haploid strains with seven chromosomes had a sexual phase with syngamy and meiosis. Again he found engulfment of one amoeba by another and interpreted this as plasmogamy. In a still later communication Sussman and Sussman (1961), studying certain diploid stocks which were heterozygous for pigment, found that haploidization occurred and that some haploid derivatives were of the parental types, whereas others were recombinant types. Heterozygosity and recombination certainly argue strongly for a sexual cycle.

On the other side of the argument Bonner (1960), using time-lapse cinephotomicrography to study the life cycles of *Dictyostelium mucoroides*, *Dictyostelium purpureum*, and *Polysphondylium violaceum*, failed to find any evidence of sexual fusions.

The controversy over sexuality is important not only in itself, but also in relation to the aggregation stage, as we shall see presently.

Aggregation. When a population has reached a certain minimum number of cells, the amoebae stop feeding and centers of aggregation are set up. The amoebae orient themselves with reference to these centers and move toward them in streams (Figures 21E-G). What stimulus causes the amoebae to behave in this fashion? What sets up an aggregation center? When a colony begins as a single, haploid cell, all progeny have presumably the same genetic constitution and the entire population should consist of similar cells. Here is an opportunity to study the problems of differentiation which have intrigued biologists for centuries.

As was stated before, Wilson (1953) and Wilson and Ross (1957) believe that zygotes formed by the union of two amoebae migrate toward the center of the colony and set up centers of aggregation toward which amoebae stream. M. Sussman and his coworkers believe that certain "initiator cells" (I cells), which they find occurring with a frequency of 1:2000 in the strain of *Dictyostelium discoideum* under observation, are responsible for setting up centers of aggregation (Sussman and Ennis, 1959). However, Konijn and Raper (1961) have showed beyond doubt that aggregation in this organism does take place in small populations of 100 or fewer myxamoebae and is independent of any recognizable special type of cell. Also, Bonner's time-lapse moving pictures of the beginnings of aggregation in *Dictyostelium mucoroides*, *Dictyostelium purpureum*, and *Polysphondylium violaceum* showed that a very few average-sized cells constituted the aggregation center in each case and revealed no

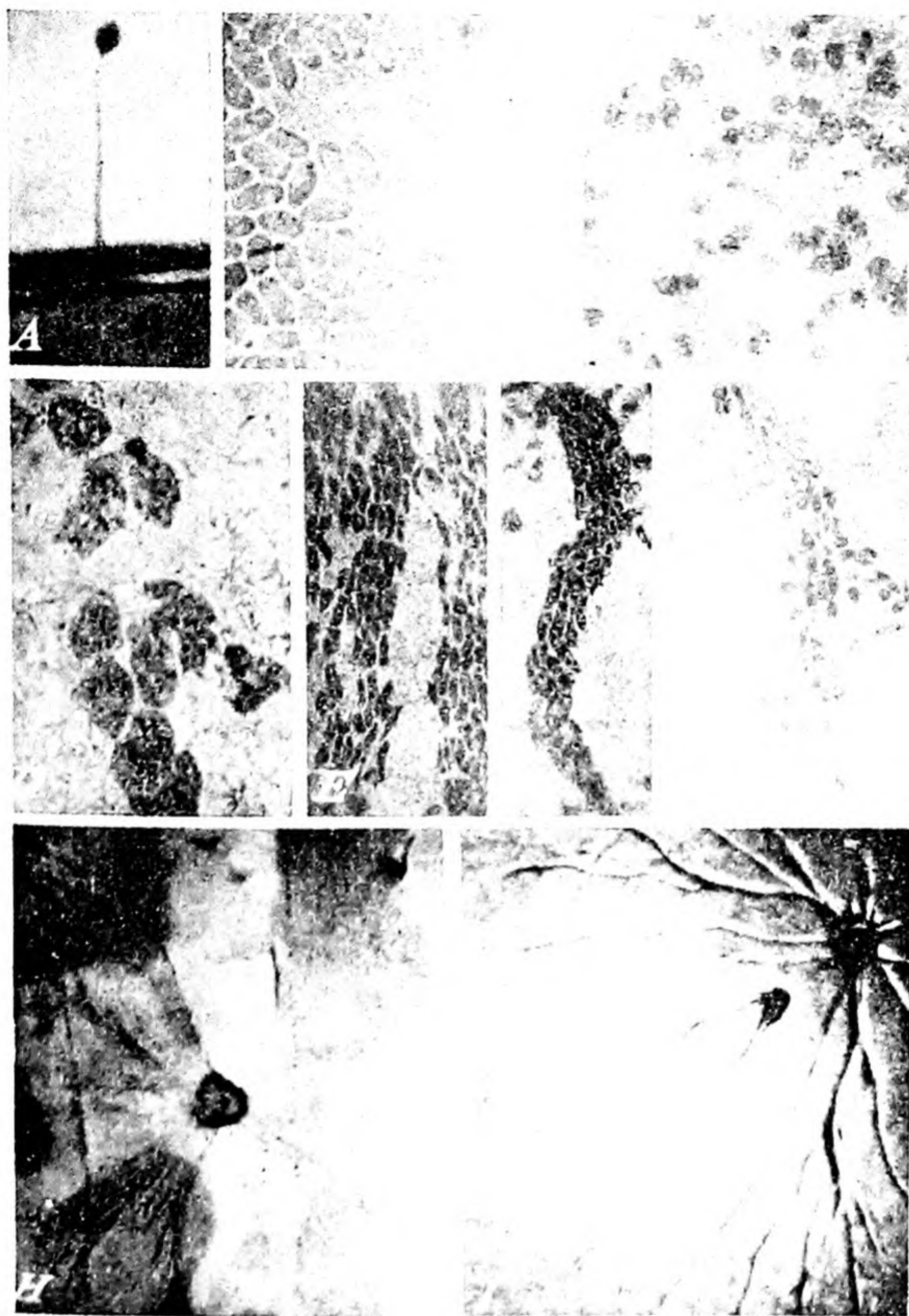


Figure 21. *Dictyostelium discoideum* Raper. A. Mature sorocarp. B. Spores. C, D. Myxamoebae. E-G. Three stages in the aggregation of myxamoebae forming a pseudoplasmodium. H, I. Pseudoplasmodia. Courtesy Raper, 1935, *Jr. Agr. Res.*, 50:135-147.



Figure 21 (Cont'd). *Dictyostelium discoideum* Raper. A. Pseudoplasmodium. B-D. Migrating pseudoplasmodium. E. Side view of pseudoplasmodium just before it ceases migration. F-K. Successive stages in sorocarp formation (G is top view of F). L. Mature sorocarp. Courtesy Raper, 1935, *Jr. Agr. Res.*, 50:135-147.

evidence of zygote formation or of the presence of large or differentiated initiator cells (Bonner, 1960).

Although the cause of aggregation is still unknown, the mechanism is now somewhat better understood. One or more cells responsible for aggregation begin to secrete a chemical substance called acrasin (Bonner, 1947; Shaffer, 1956), which attracts other cells within a certain radius, orients them toward the aggregation center, causes them to become sticky and adhere to each other, and stimulates them in turn to secrete more acrasin. Thus, acrasin gradients are set up in the immediate vicinity of the secreting cells. This is probably repeated many times from the center down in a series of rhythmical secretions, from the stream as well as the center, renewing the stimulus which causes the adhering amoebae to stream toward the center (Shaffer, 1957a, b; 1958).

There are several types of acrasin, each specific for the amoebae of one or more species. The amoebae of some species respond to one type of acrasin, whereas those of another show no reaction to it at all.

An antigen has been discovered which appears to be linked in some way with cell aggregation (Sonneborn *et al.*, 1961). It either appears at the time of aggregation or increases enormously during this stage.

The Pseudoplasmodium. As the amoebae reach the center of aggregation, they mass together to form a pseudoplasmodium. The classical experiments of Kenneth Raper, and subsequently those of J. T. Bonner and others, show that no fusion of protoplasts takes place in a pseudoplasmodium and that this structure consists of intimately associated but distinct uninucleate cells. An interesting demonstration of the individuality of the amoebae in a pseudoplasmodium was provided by Raper and Thom (1941). By grinding together in a mortar pseudoplasmodia of different species, these investigators showed that composite pseudoplasmodia and fruiting bodies could be produced, but that each spore head consisted of spores of only one species.

The pseudoplasmodium in some species, such as *Dictyostelium discoideum*, migrates for a considerable distance before it culminates into a sorocarp. In other species the change to sorocarp occurs at the point of pseudoplasmodial formation. In *Dictyostelium discoideum*, the rate of migration ranges between 0.3 and 2.0 mm. per hour at 20° C. (Bonner *et al.*, 1953). The slugs are positively phototropic and are extremely sensitive to temperature, moving toward warmer regions with a remarkable ability to detect differences of 0.0005° C. (Bonner *et al.*, 1950).

Sporulation and Macrocyts. The cells of the pseudoplasmodium become differentiated at an early stage into two types. The front of the slug consists of potential stalk cells, and the posterior portion of sporogenous cells. When migration ceases, the pseudoplasmodium becomes globose, then flattens at the base and develops a papilla. Cells of the apical region now become stalk cells and begin to push down through the whole cell mass. A cellulose cylinder is formed (Raper and Fennell, 1952) within which the stalk cells build up the stalk of the developing fructification, and, as more stalk cells are piled up, the whole cell mass rises on the newly developing stalk. The posterior cells, which are the sporogenous cells, eventually rise to the top of the fully developed stalk and are transformed into spores.

Under certain conditions which are not understood as yet, myxamoebae aggregate into pseudoplasmodia which do not form sorocarps, but instead become divided into rounded cell masses surrounded by thick cellulose walls (Blaskovics and Raper, 1957). Such structures are called macrocyts (Gr. *makros* = long + *kystis* = bladder). Their function is not known.

The Sorocarp. The morphology of the sorocarp differs in different species and is the chief basis for classification. In general, a sorocarp consists of a stalk carrying a group of spores at its tip. In some species there is a disc at the base of the stalk. The stalk may be simple or branched. If there are branches, each bears a head of spores. In some species the sorocarp is made of three or four stalks which adhere along most of their length, separating at the top, each bearing a head of spores. In the Acrasiales, the stalks of the sorocarps typically consist of cells arranged in various patterns. Only in the genera *Acytostelium* and *Protostelium* are the stalks acellular.

Classification. The order Acrasiales as now constituted is subdivided into four families: Sappiniaceae, Guttulinaceae, Acytosteliaceae, and Dictyosteliaceae. The following is an outline of the families and genera known.

order ACRASIALES

Family Sappiniaceae

Genus *Sappinia* (1 species)

Family Guttulinaceae

Genus *Guttulinopsis* (3 species)

Genus *Guttulina* (4 species)

Genus *Acrasis* (2 species)

Family Acytosteliaceae

Genus *Protostelium* (1 species)Genus *Acytostelium* (1 species)

Family Dictyosteliaceae

Genus *Dictyostelium* (6 species)Genus *Polysphondylium* (2 species)Genus *Coenonia* (1 species)

The Acrasiales are probably not related to any of the other organisms we shall discuss in this book. They appear to have their affinities with the free-living amoebae rather than with the fungi and should probably be classified with the Protozoa. They are included here only because mycologists have taken an interest in them and because they are often discussed in mycology courses.

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3 order LABYRINTHULES the net slime molds

General Characteristics. The Labyrinthulales are a small order of aquatic (mostly marine) or terrestrial organisms characterized by naked, uninucleate, spindle-shaped or oval cells which become interconnected by slime filaments along which the cells glide. The slime filaments form a net (Figure 22) which has been given the unfortunate names of "net plasmodium" and "filoplasmodium." The cells divide mitotically and sometimes encyst. What little information we have about the sporulation of these organisms will be found in subsequent paragraphs.

Occurrence and Importance to Man. The majority of species in the Labyrinthulales are marine. They are associated saprobically or parasitically with marine algae such as *Ulva*, or with higher plants

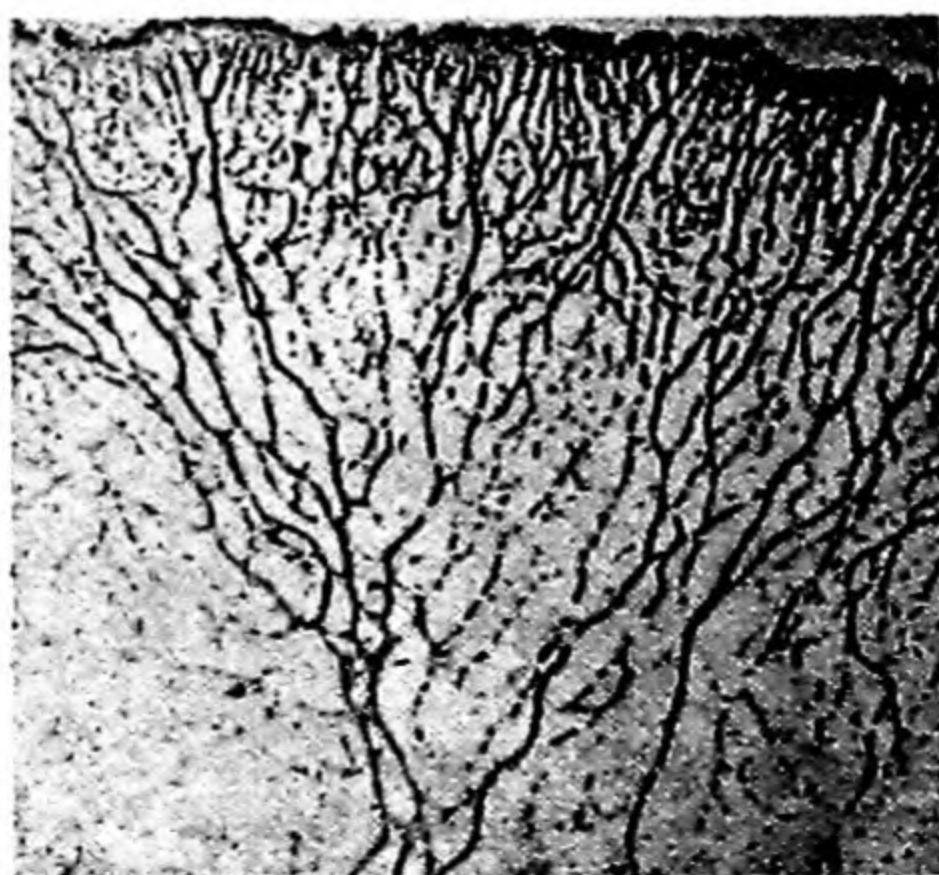


Figure 22. *Labyrinthula* sp. Net plasmodium. Courtesy Watson and Raper.

such as *Zostera*. Inasmuch as very few people have ever been interested in this group, the Labyrinthulales have been considered rare. But you will remember that the Acrasiales were also "rare" until mycologists started looking for them. It now appears that the Labyrinthulales, as a group, are quite common in marine waters, although the distribution of individual species may be restricted. As more biologists search for them, we shall learn much more than we know now about their natural habitats (Aschner, 1958).

Of the twelve known species, one is of considerable economic importance. *Labyrinthula macrocystis* is the cause of the very destructive disease of eel grass (*Zostera marina*) on both sides of the North Atlantic, as Renn (1936) has shown.

General Life Cycle. We do not have enough information on these organisms as yet to be able to construct a general life cycle with any degree of certainty. It appears (Young, 1943) that the life cycle may proceed along the following pattern. Individual spindle cells divide transversely or obliquely. When a mass of a few cells has been formed, each spindle begins to secrete a long, slimy filament from each end. As filaments from different cells come in contact, they fuse and form a network. The cells now begin to slide along the slimy tracks, usually in one direction. Several spindle cells eventually aggregate at the periphery of the net, secrete more slime tracks, and glide. The network grows and advances in this way, the cells continuing to clump at the advancing edge of the colony and in turn extending new filaments, thus perpetuating the net. At a certain stage of development many cells mass together and become enveloped in a tough membrane, forming a sorus (Gr. *soros* = heap). Eventually the soral membrane ruptures and liberates small, spherical structures (spores?) which elongate, become spindle-form, and begin producing new slime filaments.

The Cells. In all known species except one, the individual cells are spindle-shaped (Figure 23). The one exception is *Labyrinthula minuta* (Watson and Raper, 1957), whose cells are predominantly oval (Figure 24). Flagellated, heterokont (Gr. *heteros* = different + *kontos* = staff, rod) zoöspores (*i.e.*, biflagellate zoöspores with one flagellum shorter than the other) have been reported for *Labyrinthula algeriensis* (Hollande and Enjumet, 1955) and may occur in other species. The cells are uninucleate, the nuclei possessing a nucleolus and dividing mitotically during cell division, which is mostly transverse. However, in *Labyrinthula minuta*, each cell divides twice, first transversely and then longitudinally, giving rise to four cells which then usually separate before they divide again.

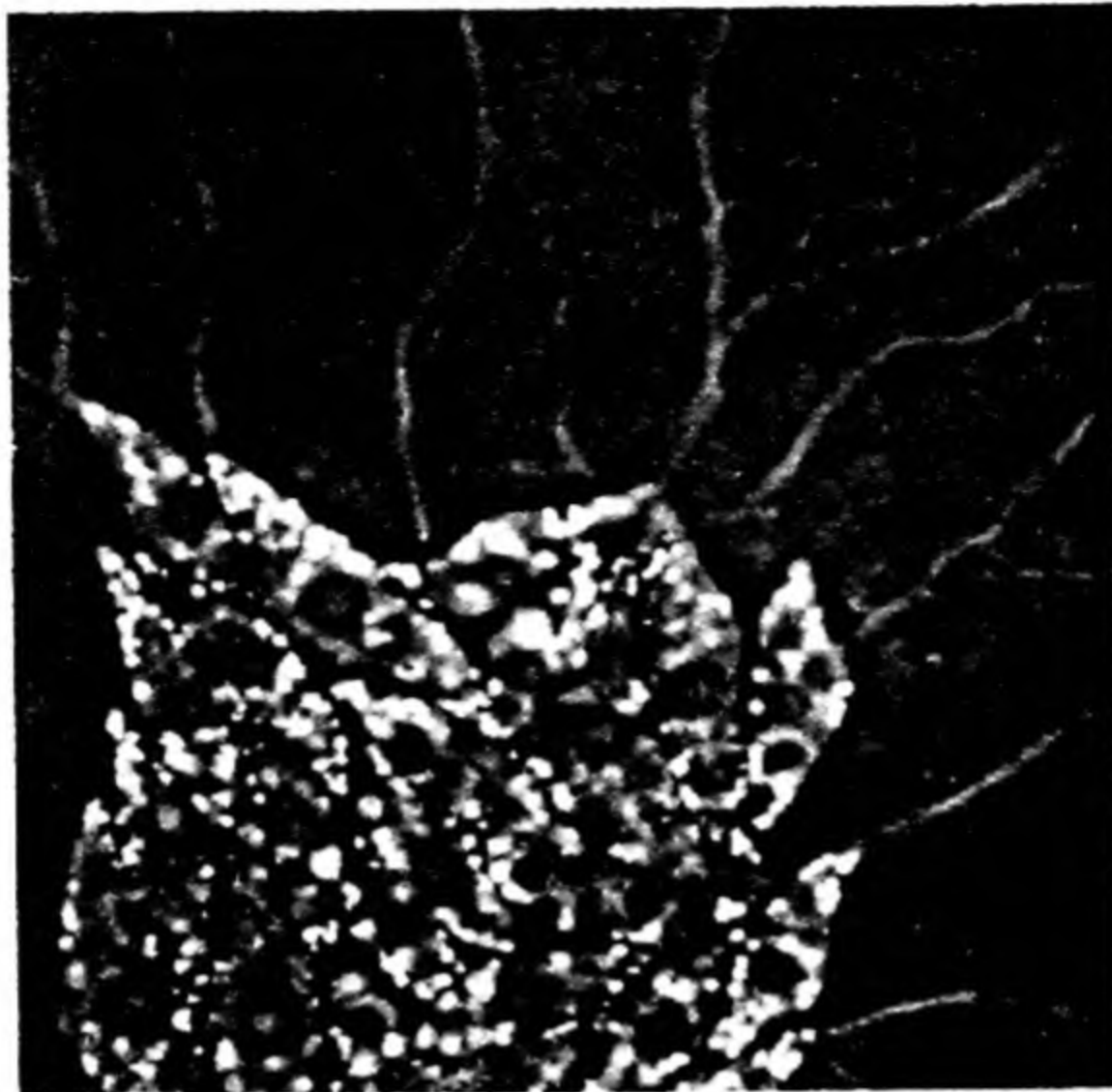


Figure 23. *Labyrinthula vitellina*. Spindle-shaped cells with slime filaments. Courtesy Watson and Raper, 1957, *Jr. Gen. Microbiol.*, 17:368–377.



Figure 24. *Labyrinthula minuta*. Oval cells with slime filaments. Courtesy Watson and Raper, 1957, *Jr. Gen. Microbiol.*, 17:368–377.

Tetrads have been observed in other species as well (Chadefaud, 1956) and may possibly originate in the same way.

The Colony. The colony is the most conspicuous and characteristic stage of the life cycle of the Labyrinthulales. When several cells have been formed, each secretes a long, slimy filament from each end. These filaments appear to sway back and forth as if they were searching for something. Whether the cell itself controls the movement of the filaments, or whether swaying is due to external forces such as currents of water, is not known. However, as a result of this motion, filaments from different cells contact one another and a network of slime tracks is formed along which the cells now glide. There is a difference of opinion concerning the nature of these slime tracks. Some students of the Labyrinthulales consider them to be tubes inside which the cells move. Others think that the cells glide on the surface of the slime tracks. Most investigators agree that the slime tracks consist of non-living matter, but others (Jepps, 1931; Chadefaud, 1956) believe that, in some species, they are filamentous pseudopodia.

In most known species, the individual cells glide along the slime tracks of the net in one direction only, never reversing themselves. In *Labyrinthula minuta*, however, the cells are capable of reversing their direction of movement (Watson and Raper, 1957). The mechanism which enables cells to glide on (or within) the slime tracks is unknown.

As mentioned before, several cells eventually aggregate at the periphery of the slime net, secrete new filaments which extend the net, and begin sliding again on the newly formed network. In this way the colony progresses.

Reproduction. As is apparent from the discussion of the general life cycle, we have little information about the reproduction of these organisms. It has been definitely established that the spindle cells divide and produce more spindle cells, but beyond this fact our knowledge is fragmentary. Hollande and Enjume (1955) describe sporogenesis in *Labyrinthula algeriensis* as follows. Numerous cells accumulate in certain places within the slime filaments. Each cell enlarges and becomes converted into a mucilaginous *sporocyte* (Gr. *sporos* = seed, spore + *kytos* = a hollow vessel, cell) in which spore groups of six, eight, or more spores are formed, surrounded by mucilaginous envelopes of their own. Thus, a slime filament (tube) contains several sporocytes, each of which contains several spore groups. The spores escape as biflagellate zoöspores, swim for a few hours, lose their flagella, secrete a delicate transparent envelope

around them, and divide actively, while their envelope develops into a slime filament which is the beginning of a new colony.

In *Labyrinthula minuta*, multinucleate bodies (plasmodia?) are formed, possibly by the enlargement and nuclear division of a single cell, and then possibly fragment into uninucleate cells which resume the life cycle (Watson and Raper, 1957). In some other species, cells mass together, become enveloped in a tough membrane, and form a sorus (Young, 1943). The membrane eventually bursts and liberates small, globose "spores," each of which grows into a spindle cell and initiates a new colony.

Sexual reproduction has not been reported in any species up to now, but the formation of tetrads, which in other organisms is often an indication of meiosis, has been observed.

Nutrition. In nature, some of the Labyrinthulales are known to be parasitic on algae and on higher plants. The cells penetrate the tissues of the host and develop inside. The life cycle is difficult to follow once the parasite has entered the host, but in some forms, at least, the network of the parasite has been observed (Jepps, 1931) within the cells of the host, moving from cell to cell. It is probable that the parasite is feeding on the protoplasm of the host.

Aschner (1958) and Aschner and Kogan (1959) grew *Labyrinthula macrocystis* on agar media with bacteria (*Escherichia coli*) and with yeast (*Rhodotorula pallida*) which the *Labyrinthula* used for food. Aschner and Kogan found that, when the peripheral cells of the net plasmodium came in contact with the food, a large system of channels developed, leading into the food source. It appears that some kind of stimulus is set up which travels down the stream and induces the amoebae to move toward the food. When the stream was interrupted, the portions of the net plasmodium which had been isolated showed no chemotropic reaction. At this time, therefore, it does not seem probable that a mechanism similar to that of cellular slime mold aggregation can be postulated to explain *Labyrinthula's* reaction to food.

Some species of *Labyrinthula* have been grown in pure culture on natural (Watson and Ordal, 1957) or synthetic media of defined chemical composition (Vishniac, 1955a). Studies of this type, in addition to giving information on the nutritive requirements of these organisms, will explain why some species are strictly marine, whereas others are fresh-water forms, and will be invaluable in understanding the ecology of these organisms. In addition, they will enable us to follow the life cycle in culture, step by step, and assist in settling the

controversial points which have been pointed out in the foregoing discussion.

Classification. Eleven species of the Labyrinthulales have been named and have been assigned to four genera by various investigators. Most of them belong to the genus *Labyrinthula*.

The French mycologist Marius Chadeffaud classified (1956) all known Labyrinthulales into two genera: (1) *Labyrinthula* consists of marine species in which the slime tracks are of non-living material secreted by the cells, and which do not feed on solid particles through phagocytosis; (2) *Labyrinthorhiza* contains the fresh-water species in which the slime tracks are living filaments. Some of these species obtain their nourishment through phagocytosis.

Whether future students of these organisms accept Chadeffaud's conclusions and classification remains to be seen. Until our knowledge of the morphology and life history of the Labyrinthulales expands considerably, classification can make little progress.

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PART III THE LOWER FUNGI

4 division
MYCOTA
sub-division
MYXOMYCOTINA
class
MYXOMYCETES
the true slime molds

Introduction. Hidebound for many years by the traditional idea that all life must be plant or animal, biologists were perplexed by the slime molds, which seemingly defied classification in either group because they exhibited some characteristics of both. The acellular, creeping, somatic phase of the slime molds is definitely animal-like in its structure and in its physiology; the reproductive structures, however, are plant-like, producing spores covered by definite walls, probably containing cellulose. De Bary (1887), one of the founders of the science of mycology, considered the slime molds to be animals and called them *Mycetozoa* (sing. *mycetozoön*; Gr. *mykes* = mushroom + *zoön* = animal). He believed that they originated independently from the bacteria, the Acrasiales, and the fungi, and treated them as a separate group. Later, Lister (1925), Hagelstein (1944), Bessey (1950), and Kudo (1954), followed De Bary in the use of the name *Mycetozoa*, Bessey and Kudo actually classifying the slime molds in the phylum Protozoa of the animal kingdom.

Thomas H. Machbride (1899), who was one of the first American monographers of this group, used the term *Myxomycetes* (Gr. *myxa* = slime + *myketes* = mushrooms, fungi), which Link had used in 1833 in accordance with his belief that the slime molds are fungi. Professor G. W. Martin of the University of Iowa, who is the world authority on the taxonomy of the slime molds and who believes that

the fungi have originated from protozoan-like ancestors, has put forth some very convincing arguments (1932, 1960/1961) for the fungal nature of the slime molds. Nevertheless, because the Myxomycetes, a very old and relatively stable group, have become quite specialized in many ways, Martin considers that they have departed sufficiently from the main evolutionary line of the fungi to constitute a subdivision of their own, the Myxomycotina. This is the view we are adopting in this book.

Occurrence, and Importance to Man. Most slime molds live in cool, shady, moist places in the woods, on decaying logs, dead leaves, or other organic matter which holds abundant moisture. A few species occur in open spaces, creeping over vegetation, and these are especially conspicuous on the grass of city lawns. Some species develop on pieces of bark taken from living trees and placed in a moist chamber for a few days.

Moisture and temperature seem to be the factors most important in governing the distribution and abundance of slime molds. During a rainy season they begin, as a class, to appear in May, in the north temperate region, and continue to fruit through October. However, not all species may be found at all times. Some are more abundant in the spring, some in the middle of the summer, others in early fall. Most of the 450 odd known species are universally distributed, but some are confined to the temperate regions, and others to the tropics.

Slime molds in general are of little direct economic importance. They feed on bacteria, protozoa, and other minute organisms. Occasionally slime molds creep over ornamentals, rendering them unsightly and, in rare instances, smothering them (White, 1933). *Phy-sarum cinereum*, one of the common Myxomycetes, may form colonies several feet in diameter on city lawns. These colonies appear bluish and may be quite conspicuous (Bonifacio, 1960). Lawn owners become disturbed about this "disease" of their lawns and write asking for advice concerning control methods. The cure is simple: mow the lawn!

In recent years, not only mycologists but also cytologists, biochemists, and biophysicists have become interested in the study of slime molds because these organisms are ideal tools for experimental studies on the mitotic cycle, morphogenesis, the chemical changes that govern reproduction, the structure and physiology of protoplasm, and a variety of other fundamental questions which challenge the scientist.

The slimy somatic phase of the slime molds, which has no cell walls, is considered the purest form of protoplasm encountered in

nature in massive quantities. As such, it is frequently employed for laboratory studies on the chemical composition of protoplasm. Even so, it is actually far from being pure protoplasm, for it contains much non-living material such as food particles or other matter which is definitely not protoplasmic.

Plasmodia and fructifications of many species of slime molds are very colorful. In addition, fructifications of most species are delicately constructed, forming intricate designs. The artistic value of these organisms was recognized some years ago, when a series of paintings depicting slime mold fructifications appeared in full color in the *National Geographic Magazine*.¹ The fructifications of *Stemonitis*, one of the Myxomycetes, attained dubious fame at the Chicago World's Fair in 1933 when placed on exhibit at the "Believe It or Not" pavilion over the caption: "Hair growing on wood—Believe It or Not." Students of mycology did not!

Classification. Organisms included in the class Myxomycetes, which constitutes the sub-division Myxomycotina of the division Mycota, have a free-living, acellular, multinucleate somatic phase, the plasmodium, which behaves as a unit at all times and eventually gives rise to fructifications. Flagellated swarm cells are produced under proper conditions, probably by all species. With the exception of the three species which are separated from all the others into a sub-class of their own (*Ceratiomyxomycetidae*), all others produce their spores inside a fructification which usually develops a peridium enclosing the spores. The Myxomycetes are subdivided into six orders on the basis of method of spore production, spore color, type of fructification produced, and lime content of the fructification. These orders are *Ceratiomyxales*, *Liceales*, *Trichiales*, *Echinosteliales*, *Stemonitales*, and *Physarales*.

SIMPLE KEY TO THE SUB-CLASSES AND ORDERS OF THE CLASS MYXOMYCETES

(Based on G. W. Martin, 1961)

- | | |
|---|--|
| A. Spores borne externally on individual stalks | Sub-class <i>Ceratiomyxomycetidae</i> (<i>Exosporeae</i>)
<i>Ceratiomyxales</i> |
| AA. Spores borne internally in fructifications | Sub-class <i>Myxogastromycetidae</i> (<i>Myxogastres</i>) |

¹ Crowder, 1926.

- B. Spores in mass pallid or brightly colored to dingy olivaceous
 - C. True capillitium and columella lacking
 - CC. Capillitium or columella characteristically present
 - D. Stalked, minute; columella present, rarely lacking
 - DD. Stalked or sessile, larger; columella never present
- BB. Spores in mass black or deep violaceous to ferruginous
 - E. Neither peridium nor capillitium calcareous
 - EE. Peridium or capillitium or both calcareous

*Liceales**Echinosteliales**Trichiales**Stemonitales**Physarales*

sub-class CERATIOMYXOMYCETIDAE
(EXOSPOREAE)

This sub-class is a very small one consisting of but three species of the genus *Ceratiomyxa*, placed in the family Ceratiomyxaceae and the order Ceratiomyxales. *Ceratiomyxa fruticulosa* is one of the

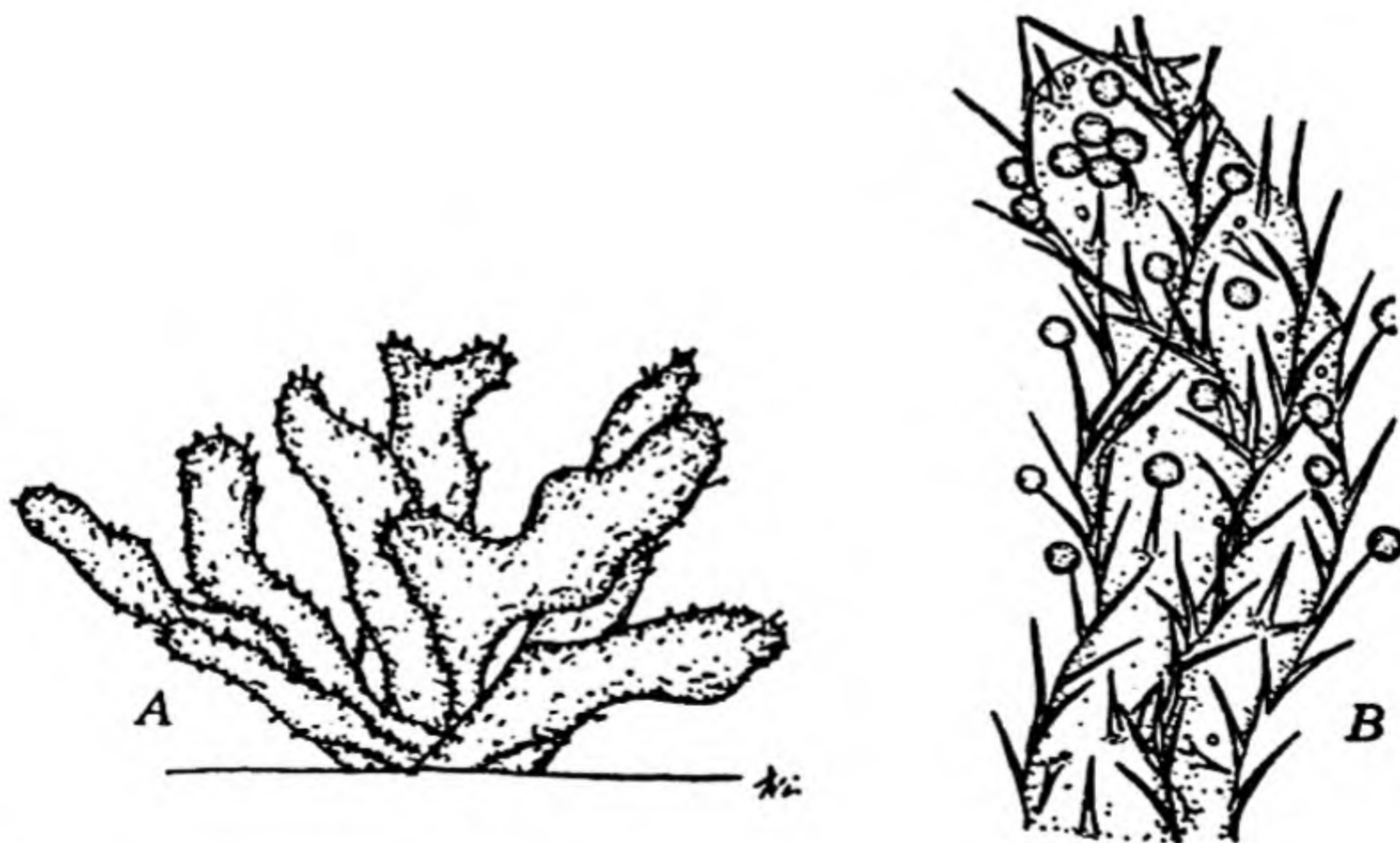


Figure 25. *Ceratiomyxa fruticulosa*. A. Fruiting body. Habit. B. Detail of single column, showing attachment of spores.

most common slime molds, world-wide in its distribution. Its life history differs in many respects from those of other Myxomycetes. Its chief characteristic is that it produces its resting spores on the surface of many white, columnar structures which compose the fructification (Figure 25). Although each resting spore has a cell wall of its own, there is no common membrane (peridium) enveloping all the spores as in the Myxogastromycetidae. Gilbert (1935) studied the life cycle of *Ceratiomyxa fruticulosa* in detail. His study indicated that the "spores" are actually one-spored sporangia, the walls of spore and sporangium being completely fused to form a single structure.

sub-class MYXOGASTROMYCETIDAE
(MYXOGASTRES)

Martin (1949) recognizes 303 species of this sub-class in his taxonomic treatise on the North American Myxomycetes. Over 400 species have been described the world over, and many more probably await discovery.

Life History. The sequence of events in the life history of the Myxogastromycetidae is usually as follows. The spores germinate under favorable conditions and produce one to four flagellated swarm cells each. Either these swarm cells may behave as gametes and copulate in pairs soon after their formation, or they may first lose their flagella, undergo a number of divisions, and then copulate. Plasmogamy is followed by karyogamy. The resulting zygote is either flagellate at first, later becoming amoeboid, or amoeboid from the start, depending on the nature of the gametes. Growth of the zygote is accompanied by a series of mitotic nuclear divisions resulting in a multinucleate plasmodium with diploid nuclei. A plasmodium may also be formed by the coalescence of many zygotes, and may continue annexing zygotes and smaller plasmodia as it develops. At maturity, the plasmodium thickens and assumes the shape of the fructification typical of the species. The nuclei now undergo meiosis with the accompanying reduction of the number of chromosomes. Each daughter nucleus, together with a portion of cytoplasm, is finally enveloped by a thick wall and develops into a spore. All this is summarized in the life history diagram in Figure 26.

There is a serious lack of life history data for the Myxomycetes as a whole, and the field is a very fertile and challenging one to the research worker interested in this group.

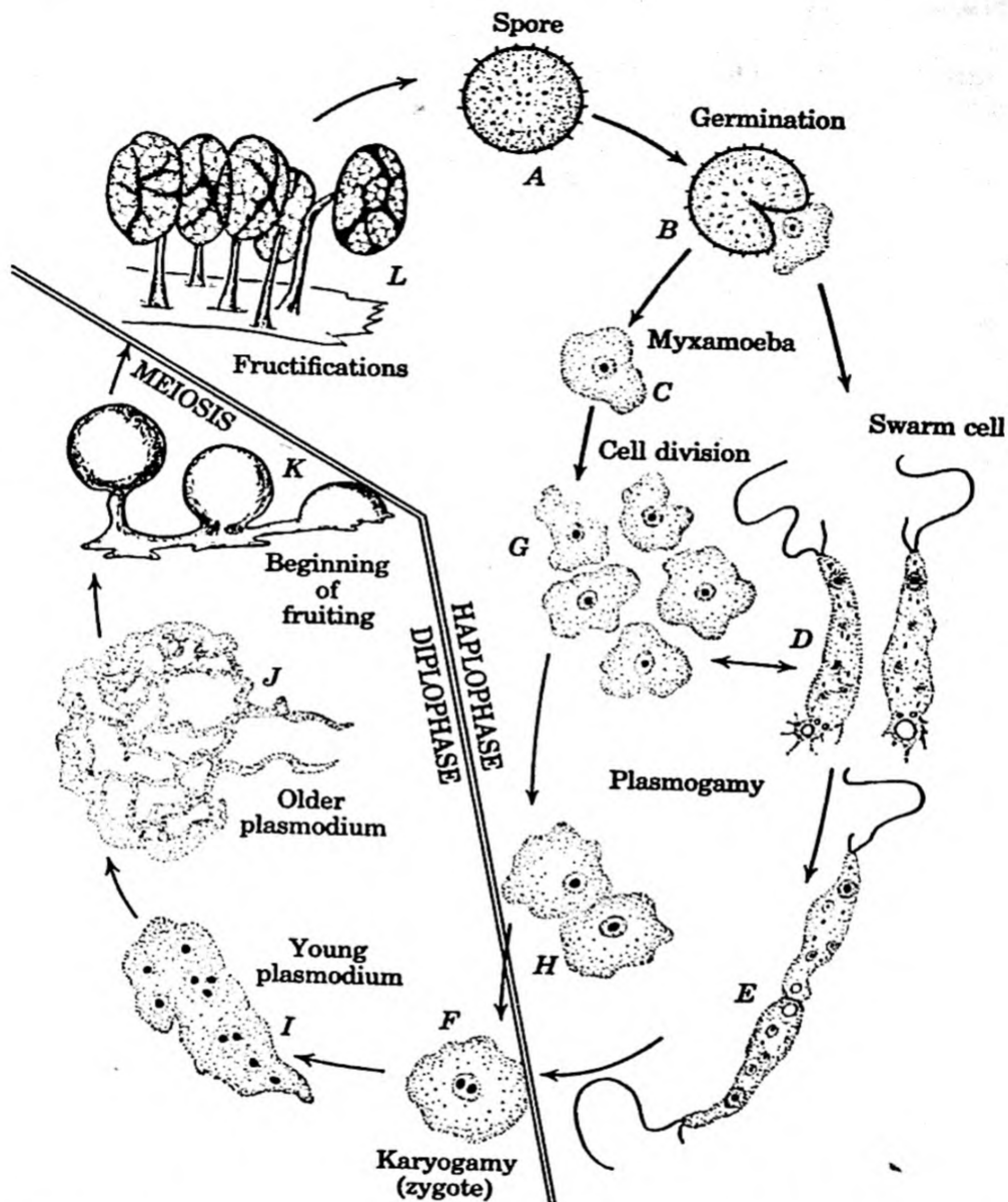


Figure 26. Life cycle of a myxomycete. D, K, redrawn from Koevenig, State University of Iowa Teachers' Guide, *Slime Molds*, 1961.

The Spore. The Myxogastromycetidae bear their spores inside a fruiting structure covered by a peridium. The spores are generally globose, with a definite, rather thick cell wall which can be smooth, spiny, warted or reticulate (covered by a network of ridges) (Figure 27). We have very little information on the composition of the spore wall. Cellulose is said to be present and chitin absent; but since no one has used modern methods for spore wall analysis, all such statements should be accepted with the greatest reservation. The color of the spores in mass may be pallid, yellow, purple, rosy, olivaceous, gray, deep violet, brown, or black. The pigments are dilute so that an individual spore, when viewed by itself under strong transmitted light, will not show the same color as the mass of spores. The spores are generally uninucleate and the nuclei typically haploid.

Spores of Myxomycetes are exceptionally resistant to unfavorable conditions, especially to prolonged periods of desiccation, which few other organisms are able to withstand. Such resistance is due to the thickness of the wall of the spore, and, no doubt, to the physico-chemical structure of the protoplasm within it. Elliott (1949) showed that spores of some species of Myxomycetes are capable of germinating after 61 years of storage in a herbarium, and if you have ever worked in a herbarium you will admit that that is quite a feat.

Factors affecting spore germination have been studied rather extensively. The papers of Gilbert (1929*a, b*), Smith (1929), Smart (1937), and Elliott (1948, 1949) revealed that the spores of most

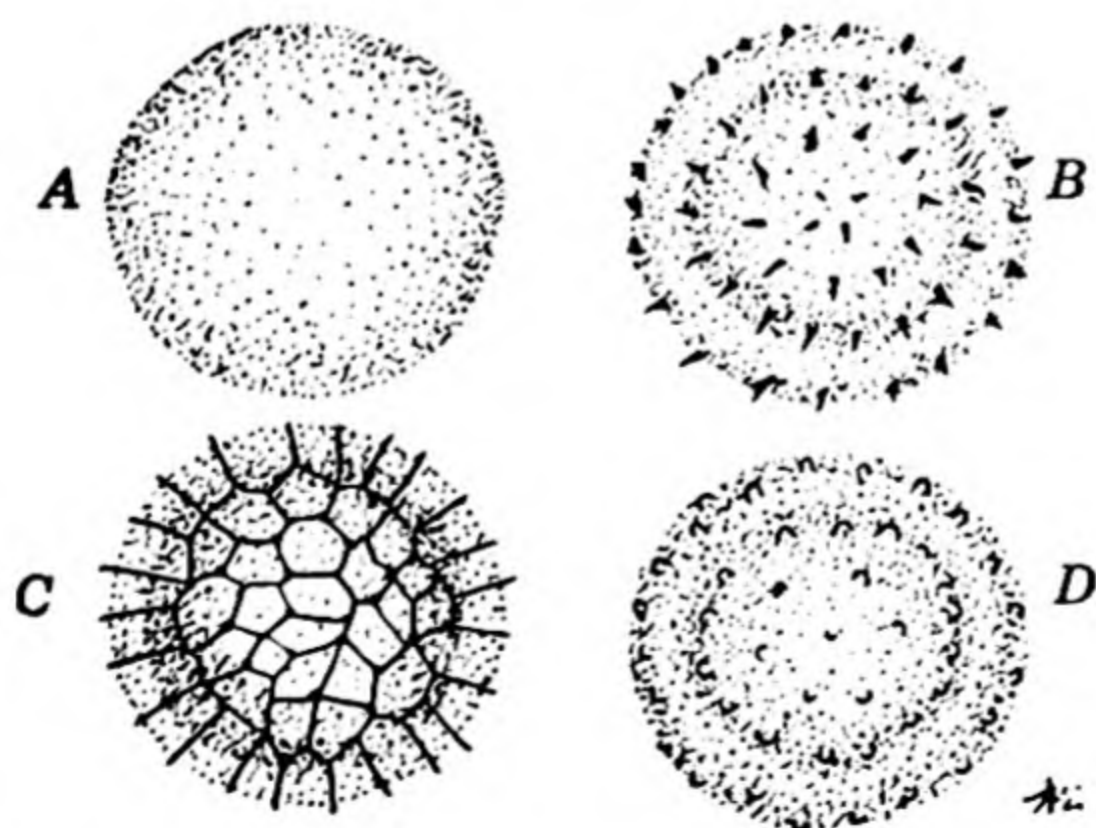


Figure 27. Four types of myxomycete spores. A. Smooth. B. Spiny. C. Ridged (reticulate). D. Warty.

species will germinate in water, especially if they are treated first with some wetting agent, such as one of the bile salts. Weak decoctions of natural substrata such as wood, bark, and hay have been found to stimulate germination in a number of species. As you would expect, temperature and pH of the medium are also factors which influence germination, as is the age of the spores. The time required for germination differs with the species. The spores of *Reticularia lycoperdon*, on the one extreme, will germinate in as short a time as 15 minutes under favorable conditions, whereas those of *Oligonema flavidum*, on the other extreme, are said to require a minimum of 14 days. Whether this behavior is due to a difference in thickness, penetrability, or chemical composition of the spore wall or to some other cause is yet to be discovered.

Swarm Cells and Myxamoebae. In nature, spores of the Myxomycetes probably germinate in rain water which has formed a dilute solution with the substratum on which the spores happen to lie. A spore germinates by one of two methods. It either cracks open or germinates by means of a tiny pore through which the protoplast emerges. The method seems to be specific for individual species. When a spore germinates, either a myxamoeba (pl. myxamoebae; Gr. *myxa* = slime + *amoeba*) or a flagellated swarm cell emerges. To a certain extent this depends on the environment. If the spores are suspended in water, the emerging protoplasts are often flagellated from the very beginning. Sometimes, however, an amoeba will issue from the spore, remain quiescent for a few minutes, and then develop flagella.

Echinostelium minutum, and perhaps other species whose spores germinate easily on the surface of moist agar in the absence of free water, is able to complete its entire life cycle without ever developing flagella (Alexopoulos, 1960). Flagellated cells, therefore, although characteristic of the Myxomycetes, are not necessary for the completion of the life cycle, at least in some species.

For many years it was thought that the swarm cells of the Myxomycetes are typically uniflagellate with an occasional cell bearing two flagella. An extensive study by Elliott in 1948, however, showed that the swarm cells of some fifty-four species (all that he studied) are typically biflagellate (Figure 28). In most of these one of the two flagella is shorter than the other. This short flagellum is often directed backward and furthermore may be appressed against the protoplasm of the swarm cell and be, therefore, rather difficult to see. Locquin (1949) arrived at the same conclusions independently. Ten years later, at the IXth International Botanical Congress, Cohen

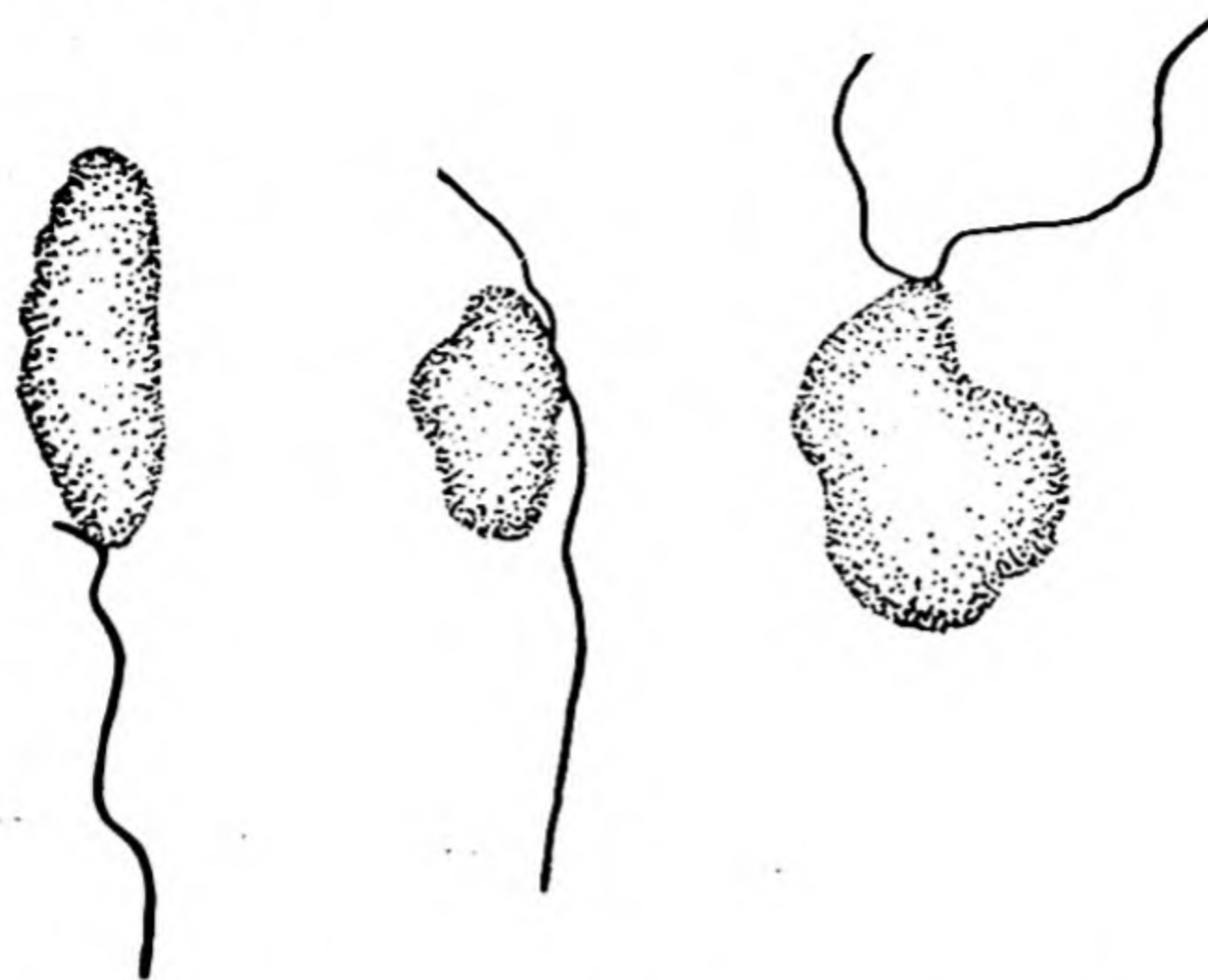


Figure 28. Swarm cells of Myxomycetes, showing variation in length of flagella. Redrawn from Elliott, 1949, *Mycologia*, 41:141-170.

(1959) reopened the question by presenting electron micrographs showing unflagellate swarm cells. University of Iowa films (1961) by Koevenig also show that unflagellate swarm cells are not uncommon. Similarly, Kole's electron micrograph (Figure 29) demonstrates that the swarm cells of *Reticularia lycoperdon* are unflagellate.

The question of flagellation, therefore, cannot be regarded as settled. It is possible that some strains of a species produce mostly unflagellate cells, other strains biflagellate. It has been shown furthermore by both Cohen (1959) and Koevenig (1961) that swarm cells produce long, flagellum-like pseudopodia which originate at the anterior end of a swarm cell and migrate down the side, eventually becoming withdrawn or absorbed. It is possible that these have been mistaken for flagella. Finally, Kerr (1960a) found that newly flagellated cells of *Didymium nigripes* are unflagellate, but may become biflagellate after several hours. Perhaps the most accurate statement of the situation at present is that myxomycete swarm cells are potentially anteriorly biflagellate, but that unflagellate cells are often produced. More extensive studies with the electron microscope should clarify the situation. As for the structure of the myxomycete flagella, our present knowledge indicates that both flagella are whiplash.

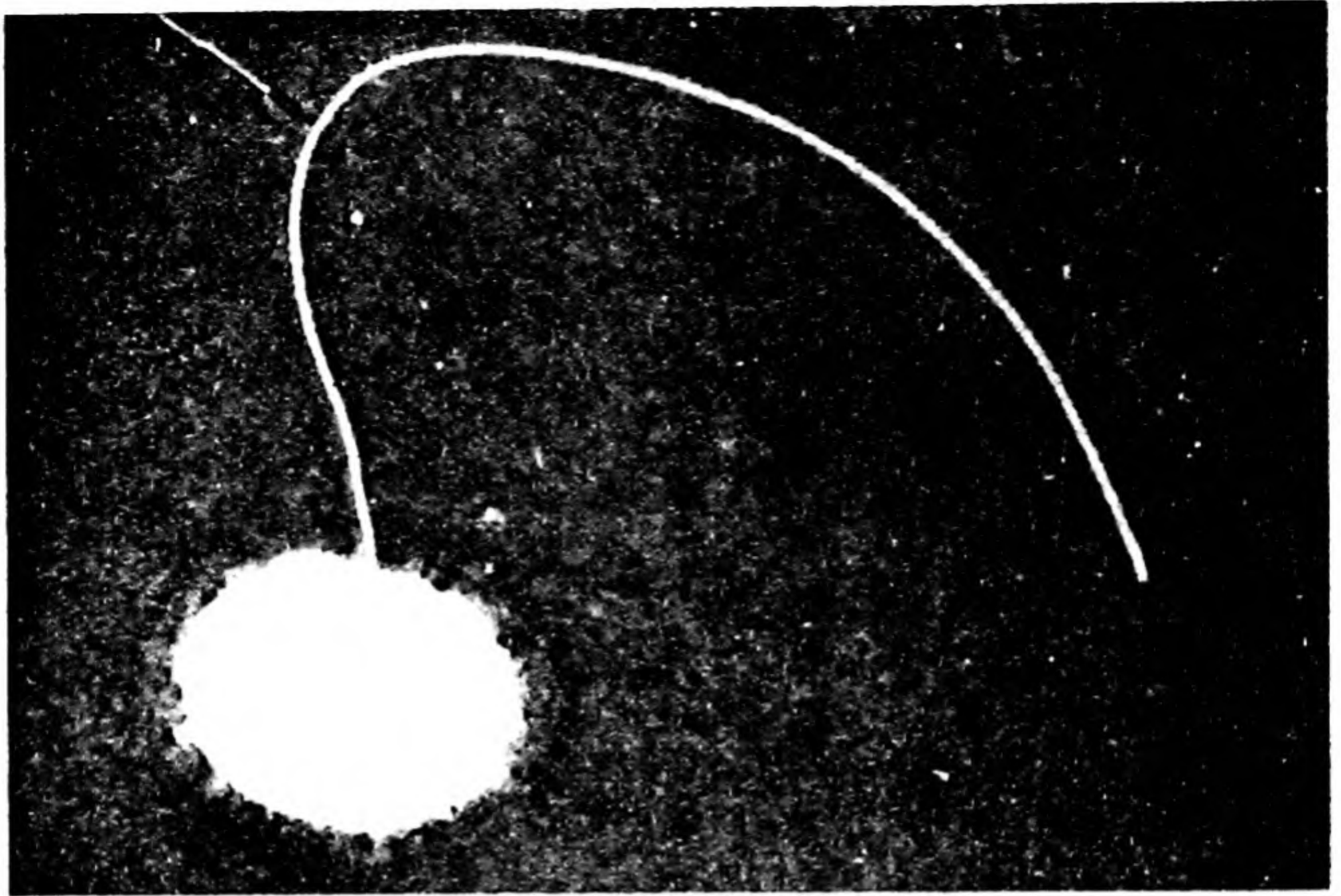


Figure 29. Electron micrograph of swarm cell of *Reticularia lycoperdon* with a single flagellum. Approx. $\times 3600$. Courtesy A. P. Kole.

After the swarm cell escapes from the spore case, it swims about with a rapid rotary movement which is combined with amoeboid contractions. At this stage it obtains nourishment by absorbing dissolved food material from the surrounding medium (Gilbert, 1928*a*, *b*) and by ingesting, at its posterior end, bacteria which it engulfs by means of pseudopodia. The posterior end of a swarm cell is very sticky and appears to be quite important both in catching food (Koevenig, 1961) and, as we shall see later, in reproduction. Yeasts, fungal spores, and particles of organic matter which can serve as food are readily ingested, in addition to bacteria, upon contacting the posterior end of the swarm cell. Food vacuoles are formed around such particles. The fact that indigestible as well as digestible matter is ingested—the former being eventually egested—may be an indication that the swarm cell does not have the power of selecting its food.

After a period of motility, the swarm cell eventually withdraws its flagella, thus changing into a myxamoeba. Under unfavorable conditions myxamoebae round up and encyst. When favorable conditions return, the cysts germinate and a myxamoeba or swarm cell

emerges from each. When food is abundant and environmental conditions are favorable, myxamoebae divide repeatedly, giving rise to a large population of haploid cells.

Sexual Fusions. Whether the term sexual should be applied to the fusions which take place between haploid cells of Myxomycetes is a matter of opinion. Martin (1940) has revived the term *karyallage* (Gr. *karyon* = nut, nucleus + *allage* = change) to refer to fusions between morphologically similar cells, preferring to restrict the term sexual to the fusions between cells which can be differentiated into male and female. In this book, however, we have adopted the view that any fusion of two haploid cells which results in the formation of a diploid zygote may be termed sexual.

In the Myxomycetes which have been investigated, such fusions take place either between flagellated swarm cells or between myxamoebae into which swarm cells have changed after withdrawing their flagella. Whether one and the same species may employ both of these methods, or whether some species employ the first and others the second, has been a matter of controversy. Kerr (1961) and Koevenig (1961) have settled this question for *Didymium nigripes* and *Physarum gyrosum*, respectively, by showing that fusions take place between both flagellated and non-flagellated cells in the two species. In *Stemonitis fusca* it is said that copulation takes place only between a swarm cell and a myxamoeba, the latter flowing into the former and producing a flagellated zygote (Benedict, 1962). These observations must be confirmed before they are accepted, in view of previous contradictory evidence.

A genetic explanation of gametic fusions in the Myxomycetes is just beginning to emerge. *Physarum polycephalum* is apparently heterothallic¹ (Dee, 1960). Collins (1961) has shown that *Didymium iridis* is heterothallic and that *Fuligo cinerea* is homothallic. Certain interesting complexities in the heterothallic species, however, indicate that many more studies of monosporous cultures are needed before the situation is clarified.

The Zygote. The zygote of a myxomycete is thus formed by the union of two planogametes (swarm cells) or two myxamoebae. Contact of planogametes takes place at their posterior ends while they are swimming with a rotary movement. If the zygote is formed by

¹ The term heterothallic is not etymologically accurate in this connection. The thalli (plasmodia) are diploid, and each nucleus contains both mating type alleles. By extension, however, a heterothallic myxomycete is one which does not form plasmodia unless gametes (swarm cells or myxamoebae) of opposite mating types fuse.

the fusion of swarm cells, it is, of course, flagellate and swims for a time before retracting its flagella and changing into a myxamoeba. As the zygote grows, its nucleus undergoes successive mitotic divisions and the zygote gradually becomes transformed into a multinucleate amoeboid structure, the plasmodium.

It appears that in some species a plasmodium is formed by the coalescence of many zygotes. Possibly the same species may form the plasmodium either by the growth of a single zygote or by the coalescence of many zygotes according to circumstances.

The Plasmodium. Being a mass of protoplasm, delimited only by a thin plasma membrane, the plasmodium does not have a definite size or shape. At one time it is globose, at another it is flat and sheet-like spreading over a large area in the form of a very thin network which is often brilliantly colored. Ever changing, ever flowing, the plasmodium creeps over the surface of the substratum, engulfing particles of food in its way. Eventually it matures and changes into the fructification typical of the species. Camp (1937), who studied the formation and structure of plasmodia of *Physarum polycephalum*, concluded that the protoplasm of a plasmodium is an apparently structureless substance with granules, vacuoles, and various other bodies embedded within it. He found that the viscosity of the protoplasm not only differs in various sections of the same plasmodium, but also changes constantly with modifications in the internal and external environments. The protoplast is fluid in some portions and gelatinous in others, the two phases blending gradually. The fluid portion of the protoplast is usually in the form of an intricately branched network streaming through the gelatinous portion of the plasmodium.

The streaming of the protoplasm in the veins of a plasmodium is a fascinating process to watch under the microscope. If you will focus the low-power objective on one of the veins of a vigorously growing plasmodium, you will see the protoplasmic granules flowing in one direction at what appears to be a great speed. And, actually, such streaming is comparatively rapid. Kamiya (1950b), investigating the rate of flow in *Physarum polycephalum*, reports that the maximum speed reached was 1.35 mm. per second which, he says, is "the greatest velocity of protoplasmic flow ever recorded." But keep your eye on the ocular for 50 or 60 seconds, and you will see that the river of protoplasm slows down, comes to a momentary stop, and then begins to flow in the opposite direction for a certain length of time, only to reverse itself again and again. This more or less rhythmical reversal in the direction of protoplasmic flow within the veins of a plasmodium

is a well-known phenomenon. Surprisingly enough, a study of the relation of this phenomenon to the direction in which the whole plasmodium is creeping reveals (Kamiya, 1950a) that the flow toward the direction of movement of the plasmodium does not necessarily last longer than the flow in the opposite direction. As a matter of fact, the progressive flow in some cases lasts a shorter time than the regressive flow. There seems, therefore, to be no close correlation between the duration of flow in any direction and the protoplasmic volume transported in the same direction.

Among the most significant findings relative to the problem of the streaming of protoplasm in a plasmodium are those of Loewy (1952), Ts'O and his coworkers (1956, 1957), and Takeuchi and Hatano (in Kamiya, 1959). These discoveries center around **myxomyosin**, a contractile protein which was found to be present in the plasmodium of *Physarum polycephalum*. Myxomyosin is a rod-shaped molecule 4000–5000 Å long with a molecular weight of 6 million. It behaves like actomyosin in animal muscle, changing its viscosity when ATP¹ is added. Furthermore, the presence of ATP itself has been demonstrated in the plasmodium, and its effect on animal muscle is the same as that of muscle ATP.

At least three general types of plasmodia are now known (Alexopoulos, 1960/1961). The most primitive type is the **protoplasmodium** (Gr. *protos* = first + *plasmodium*), characteristic of certain minute species (*Echinostelium minutum*, *Licea parasitica*, *Clastoderma debaryanum*, etc.). Such a plasmodium remains microscopic throughout its existence. It is more or less homogeneous, it forms no veins, and it exhibits a very slow, irregular streaming instead of the rapid, rhythmical, reversible streaming of the other plasmodial types. A protoplasmodium gives rise to but a single sporangium when it fruits (Figure 30).

The **aphanoplasmodium** (Gr. *aphanes* = invisible + *plasmodium*) resembles a protoplasmodium in its initial stages, but soon elongates, branches, and becomes a network of very fine, transparent strands. The protoplasm is not very granular, and the plasmodium is difficult to see. The veins are not conspicuously differentiated into gelified and fluid regions, and the streaming protoplasm seems to be confined by a very delicate membrane. Streaming is rapid and rhythmically reversible (Figure 31).

The **phaneroplasmodium** (Gr. *phaneros* = visible + *plasmodium*), characteristic of the Physarales, also resembles a protoplasmodium

¹ Adenosin triphosphate.

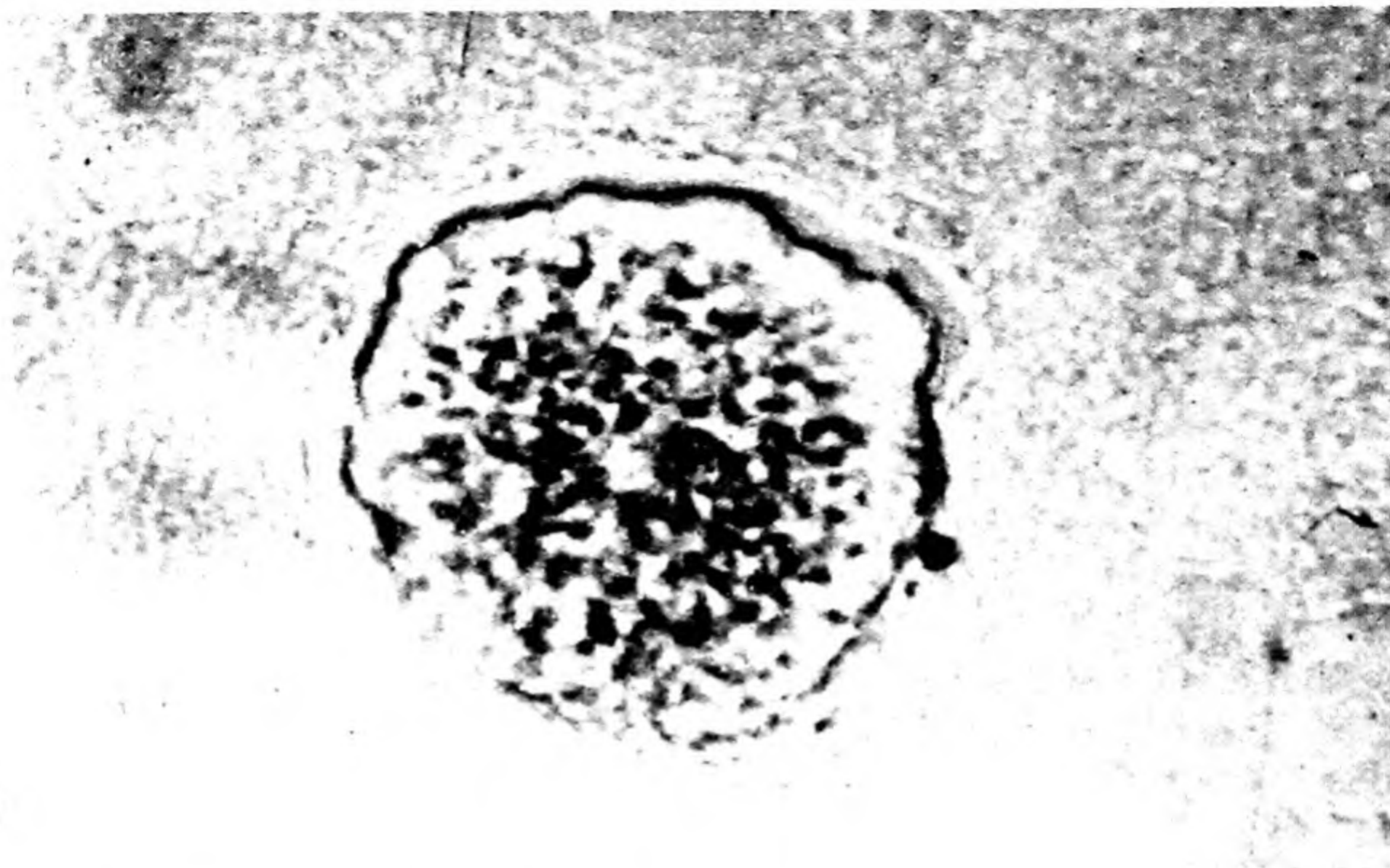


Figure 30. Protoplasmodium. (*Echinostelium minutum*.) $\times 1200$. Photomicrograph by the author.

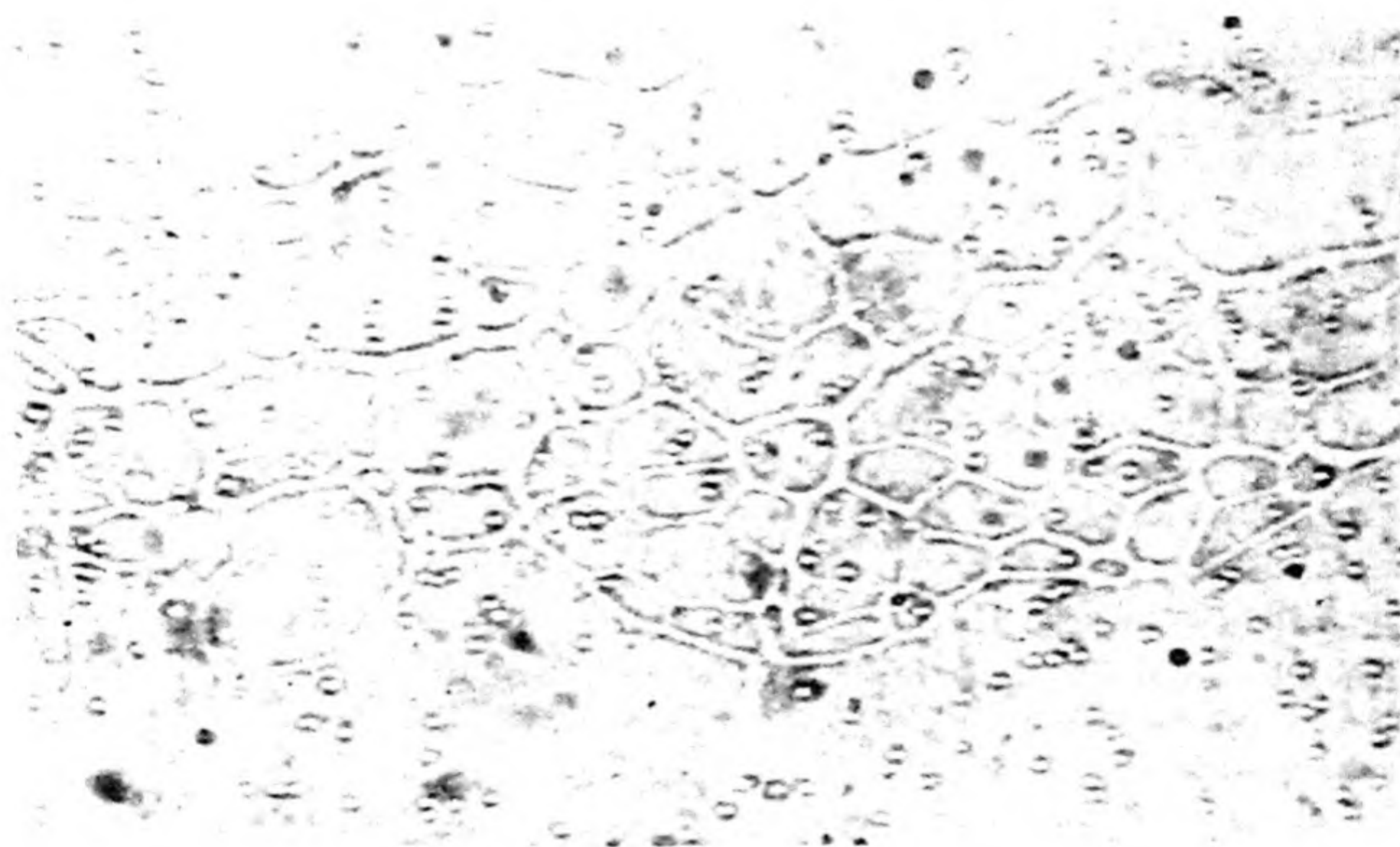


Figure 31. Aphanoplasmodium. (*Stemonitis fusca*.) $\times 250$. Photomicrograph by the author.

at first. Soon, however, it grows larger and becomes more massive. Its protoplasm is very granular, and the plasmodium is easily visible even at an early stage of development. The gelified and fluid portions of the veins are easily distinguishable, and the rhythmic, reversible streaming is very conspicuous (Figure 32).

Slime mold plasmodia are of various colors, ranging from colorless to white, gray, black, violet, blue, green, yellow, orange, and red, the color depending in part upon the species. The yellow and the white plasmodia are probably the most commonly encountered. Color changes have been observed to occur in the same plasmodium under



Figure 32. Plasmodium of *Physarum polycephalum* growing on agar. (Phanero-plasmodium.) $\times 1$. Photograph by Philip G. Coleman.

laboratory conditions and have also been induced artificially by various means. We know, for example, that in some plasmodia the pigments responsible for the color are in the nature of chemical indicators and that their color changes with variations in the hydrogen ion concentration of the plasmodium. Pigmented food particles may also be responsible for the color of a plasmodium. For example, it has been determined experimentally that the ingestion by plasmodia of cells of *Serratia marcescens*—a bacterium which possesses a red or pink pigment—imparts a reddish or pink color to the plasmodium.

Young plasmodia unite readily with other plasmodia or with zygotes of the same strain and thus increase in size. Such unions are probably somatic and are not followed by nuclear fusions.

That plasmodia of different species will not unite was recognized by De Bary (1887) and has been confirmed so often that a fusion test had been used to determine the identity of species. It was believed that non-fusion was proof that the species concerned were different. Skupienski (1934, 1939), however, showed that *Didymium iridis* and *Didymium squamulosum* consisted of physiological races whose plasmodia would not fuse one with another. Yet there was no doubt that all were somatic phases of the same morphological species. Gray (1945) later found that *Physarum polycephalum* is also composed of a number of physiological races. When he placed plasmodia of this species, isolated from different localities, in contact with each other, some fused, but others did not. Such plasmodia were similar morphologically, but different physiologically. Work in our own laboratory shows that many other species, perhaps all, are made up of physiological races. Of considerable interest are some results (Alexopoulos and Zabka, 1962) which indicate that, whereas myxamoebae of two different races of the same species (*Didymium iridis*) unite to form zygotes, the plasmodia of the two parents will not fuse with each other. Haploid protoplasts thus appear to be compatible, whereas diploid protoplasts seem to be incompatible.

Nutrition and Culture. Growth of plasmodia necessarily involves the intake of food and the excretion of waste products. In nature plasmodia probably feed on bacteria, spores of fungi and green plants, and possibly on protozoa and even on bits of non-living organic matter. They also frequently envelop and consume the fruiting bodies of shelf fungi and mushrooms. In the laboratory, the plasmodia of some species can be kept growing vigorously for a long time on a diet of finely ground oats, oatmeal, or oatmeal agar.

Actually, very little is known about the nutrition of the Myxomycetes. It is well established that swarm cells and plasmodia feed on microorganisms of various types and that they thrive better on some organisms than on others. Also, some species are known to survive on organic matter in the absence of living organisms. No extensive studies are extant, however, on the nutritive requirements of the slime molds. The chief difficulty here lies in obtaining pure cultures of the Myxomycetes. A number of investigators have succeeded in culturing various species of Myxomycetes on artificial media and have induced them to complete their life cycles from resting spore to resting spore in culture. Authentic reports of pure cultures of Myxomycetes, however, are rather rare in the literature, for it appears to be quite difficult to purify plasmodia from bacteria.

Cohen (1939) was the first to apply rigid controls to test whether cultures which appeared to be pure were indeed so. He succeeded in growing several species in pure culture in the absence of other living organisms, but had difficulty in maintaining the vigor of his cultures over a long period of time. Miss Johanna Sobels (1950), working in Holland with plasmodia isolated from natural substrata, concluded that some species of Myxomycetes are either parasitic or saprobic according to circumstances and can be purified and grown in pure culture with comparative ease. Other species seem to be obligately parasitic and soon die in the absence of living microorganisms which they can utilize for food. Miss Sobels further discovered that the plasmodia of certain species produce soluble antibiotics which inhibit the growth of certain bacteria and yeasts in culture.

A great step in the study of the Myxomycetes was taken when Dr. H. P. Rusch and his associates at the University of Wisconsin (Daniel and Rusch, 1961; Kelley *et al.*, 1960) succeeded in growing *Physarum polycephalum* in a chemically defined, liquid medium. This work made possible exact studies on the nutritive requirements of this organism (Daniel *et al.*, 1961).

Although, as mentioned above, we know that some plasmodia may absorb food in the liquid state from their substratum, the ingestion of solid particles is probably the more usual method of food intake. The process of ingestion was described by Camp (1937) as follows: "When the plasmodium comes in contact with the food particle, the latter tends to be pushed forward, away from the plasmodial margin. However, that part of the plasmodium directly behind the food ceases its forward movement while . . . on either side and above and below, the protoplasm flows out for a slight distance and tends

to surround the food particle.”¹ Thus, the plasmodium of the Myxomycetes ingests its food by the same method which protozoa such as the amoeba employ. The protoplasm no doubt secretes enzymes into the food vacuole, and these convert the ingested food particle into simpler soluble materials which the protoplasm eventually absorbs and assimilates.

The plasmodium eliminates its waste products by depositing waste particles on the substratum and moving away from them. In some instances, according to Camp, the plasmodium forcibly ejects solid particles by a contractile movement, and throws them some distance away.

Assimilation of food into the plasmodium makes growth possible. Growth is accompanied by the successive division of the nuclei embedded in the cytoplasm. Howard (1931) found that, in growing plasmodia of *Physarum polycephalum*, nuclear division occurs almost simultaneously throughout the plasmodium and requires 20–40 minutes for completion. Centrosomes and astral rays are lacking. Each nucleus contains several nucleoli, and the nuclear membrane persists throughout nuclear division.

Under carefully controlled conditions, this same organism in pure, liquid, shake cultures forms many tiny plasmodia each of which has its own rhythm of synchronous mitoses. When two such plasmodia are permitted to fuse, all the nuclei in the resulting plasmodium divide synchronously after an adjustment period of about 7–8 hours. Nuclear divisions are followed by a great increase in DNA² synthesis (Nygaard *et al.*, 1959). Since the plasmodium of the Myxomycetes develops from the growth of the zygote, or from the coalescence of many zygotes, all nuclei are diploid. A mature plasmodium which is about to enter the fruiting stage contains from fewer than one hundred to many thousand nuclei, all of which may be derived from the successive mitoses of the original zygote nucleus and its progeny.

Sclerotia. In the normal course of events, the plasmodium gives rise to a fructification. Under certain conditions, however, the plasmodium becomes converted into an irregular hardened mass, the sclerotium, which can remain dormant for a long time, but which grows out into a plasmodium again when conditions favorable for growth return. Some Myxomycetes overwinter in the sclerotial condition, as evidenced by the fact that we can find their sclerotia in the

¹ Quoted by permission of the Torrey Botanical Club.

² Deoxyribose nucleic acid.

soil, under fallen logs, or under tree stumps during warmer spells in the winter when the ground surface thaws sufficiently to permit observations. In Michigan I have collected sclerotia of *Physarum polycephalum* during such thawing periods in January, and without difficulty have grown the plasmodia from them in the laboratory.

Sclerotia may be induced to form in the laboratory by drying plasmodia gradually. They can be kept in the refrigerator or even at room temperature until needed, when they can again be placed on suitable moist media for growth.

Jump (1954), in what is probably the best study on sclerotization, found that all sclerotia are composed of small "cells" which he termed macrocysts. These vary in size from 10 to 25 μ and in the number of nuclei they contain (0-14). Each macrocyst is surrounded by a membrane. According to Jump, the process of sclerotization goes through the following stages: (1) cessation of streaming, (2) gelation of the whole plasmodium, (3) distribution of nuclei, (4) depositing of macrocyst walls, (5) completion of macrocyst formation, (6) hardening of sclerotium, and (7) shrinkage of nuclei to one-half diameter. The reconstitution of the plasmodium from a sclerotium reverses the foregoing process.

Sporulation. In passing from the somatic to the reproductive phase, the entire plasmodium of the Myxomycetes is usually converted into one or more fruiting bodies (Figure 33), so that the somatic and reproductive phases are seldom coexistent in the same individual.

The factors directly responsible for fructification in the Myxomycetes are not well understood. Moisture, light, temperature, pH, and exhaustion of food supply have all been related to fruiting by some investigators and denied by others on the basis of contradictory laboratory experimental results. Seifriz and Russell (1935) even postulated a reproductive rhythm independent of these factors for *Physarum polycephalum*. The work of Gray has shed some light on this subject. Dr. Gray (1939) found that the fruiting of *Physarum polycephalum* is influenced by both pH and temperature and that these two factors are closely related and interdependent. Within certain limits, the higher the temperature at which a plasmodium is growing the greater the acidity required to induce fruiting. Gray (1938) also showed that light is necessary for the fruiting of *Physarum polycephalum* and certain other species with yellow plasmodia, and that this factor is independent of pH and temperature. The work of Johanna Sobels and Henderica van der Brugge (1950)

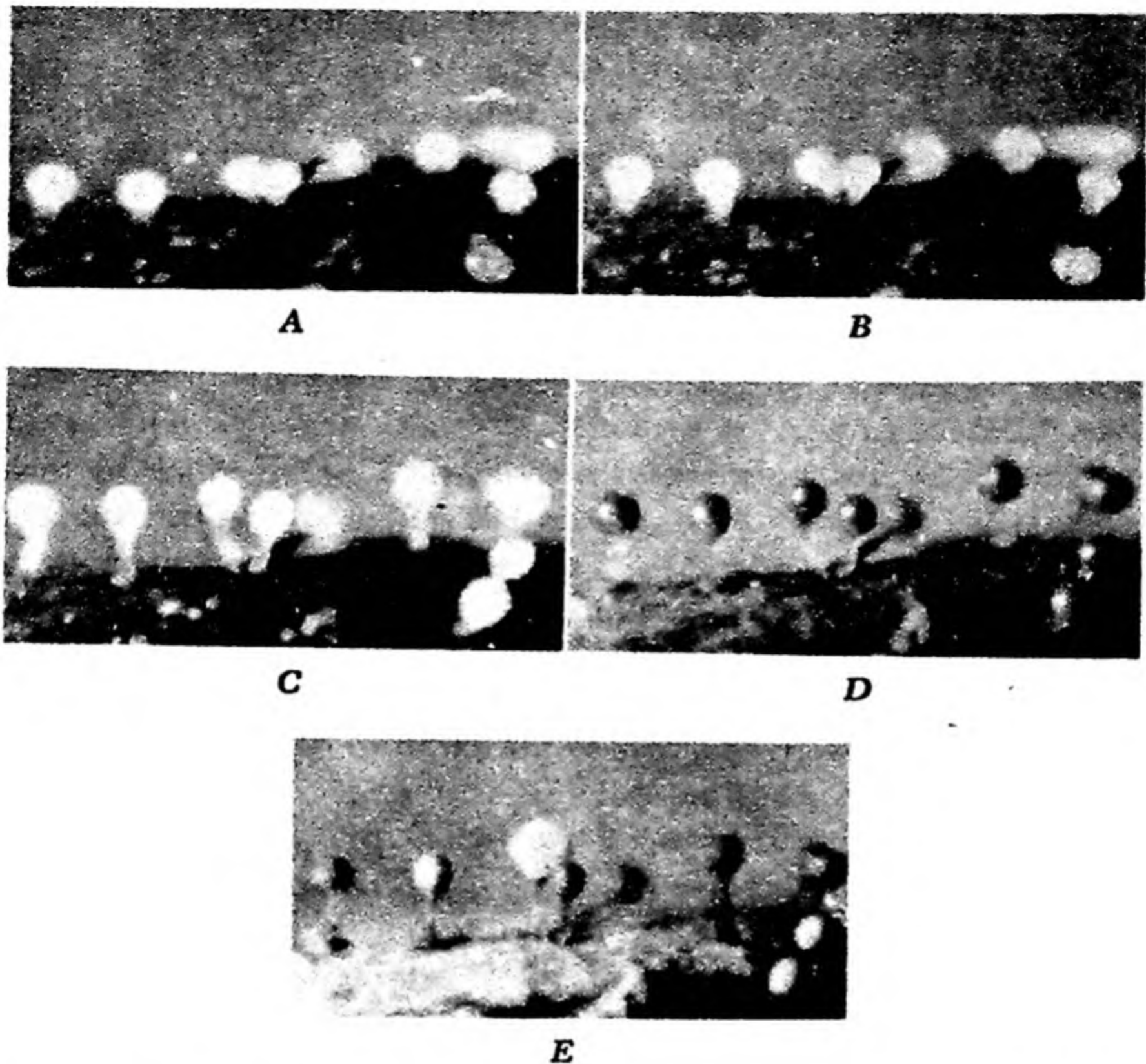


Figure 33. *Hemitrichia stipitata*. Five stages in the development of the sporangia. Courtesy J. L. Koevenig.

supports Gray's conclusions with respect to the effect of light on fruiting of pigmented plasmodia. A number of researchers have also shown that the shorter wave lengths of light are most effective. Some of the pigments in a plasmodium appear to be photoreceptors which absorb large amounts of shortwave light at low pH values (Wolf, 1959), thus explaining the effectiveness of both blue light and acidity for fruiting.

Of particular interest are the results obtained with *Physarum polycephalum* grown in bacteria-free culture (Daniel and Rusch, 1962). Plasmodia were grown in a liquid medium in the dark, harvested, and transferred to the surface of a filter paper in contact with a chemically defined liquid sporulation medium containing various inorganic salts, citric acid, niacin, and niacinamide. The conditions which favored sporulation were an optimal age of the

culture at harvest time, an additional dark incubation period, and a subsequent period of illumination.

The presence of niacin, niacinamide, or tryptophan in the medium during the postgrowth period was necessary for sporulation. Light was indispensable. The activating wave lengths of light fell in the range of 310–500 $m\mu$ with the shorter wave lengths appearing to be more favorable.

Whatever happens in a plasmodium that causes it to fruit appears to be irreversible, for once a plasmodium reaches the fruiting stage it cannot be induced to resume growth. Exactly what the changes are we do not know as yet, but a number of investigations are producing some interesting results (Ward, 1955, 1958; Nygaard, Güttes, and Rusch, 1959).

The Fructification. Three types of fructifications are formed by Myxogastromycetidae. In the first of these, the plasmodium forms numerous individual sporangia (Figures 34, 37, 39, 40) generally crowded together on the portion of the substratum formerly occupied by the plasmodium. Each sporangium has a peridium of its own.

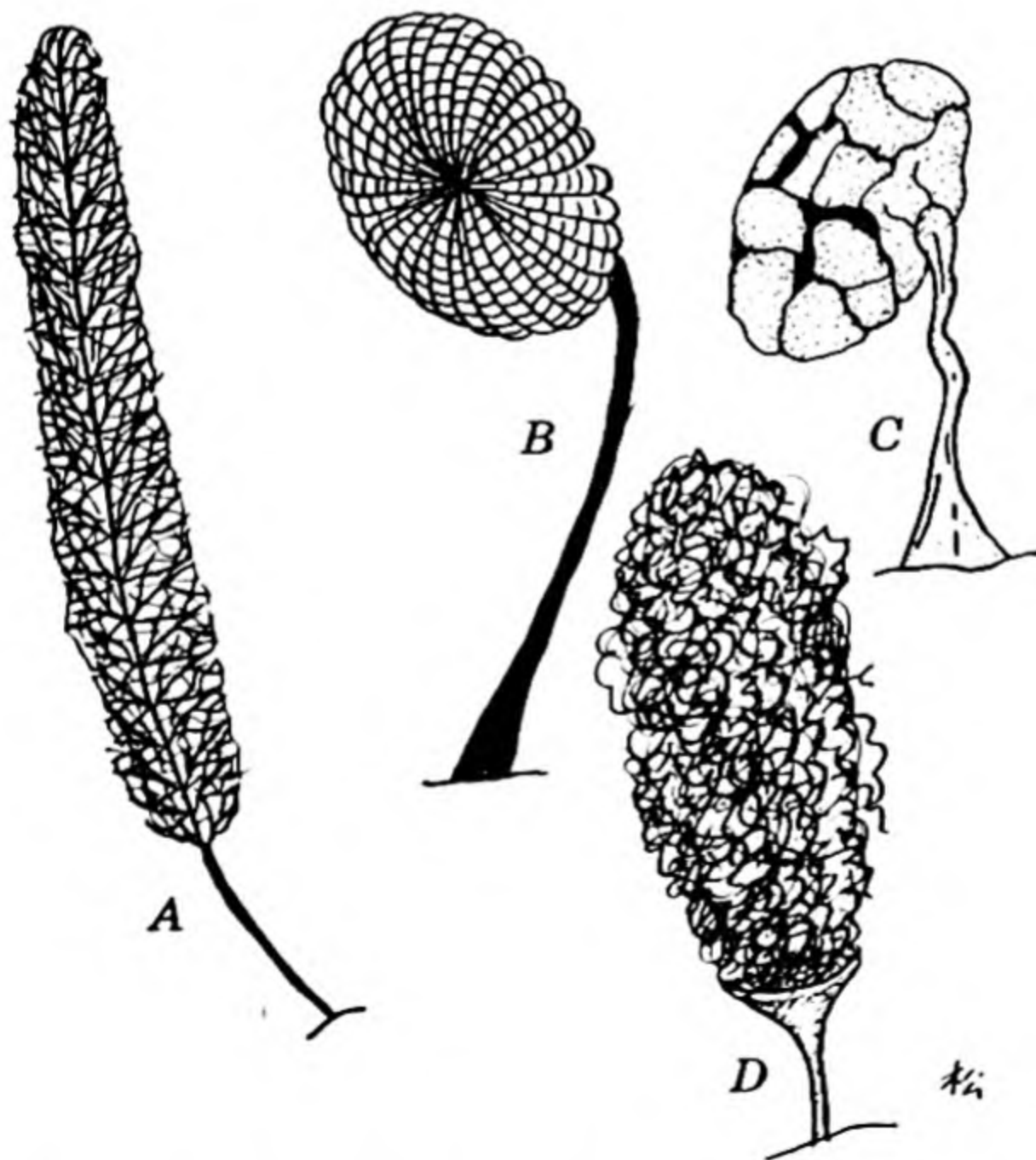


Figure 34. Four types of sporangia typical of four genera of Myxomycetes. A. *Stemonitis*. B. *Dictydium*. C. *Physarum*. D. *Arcyria*.

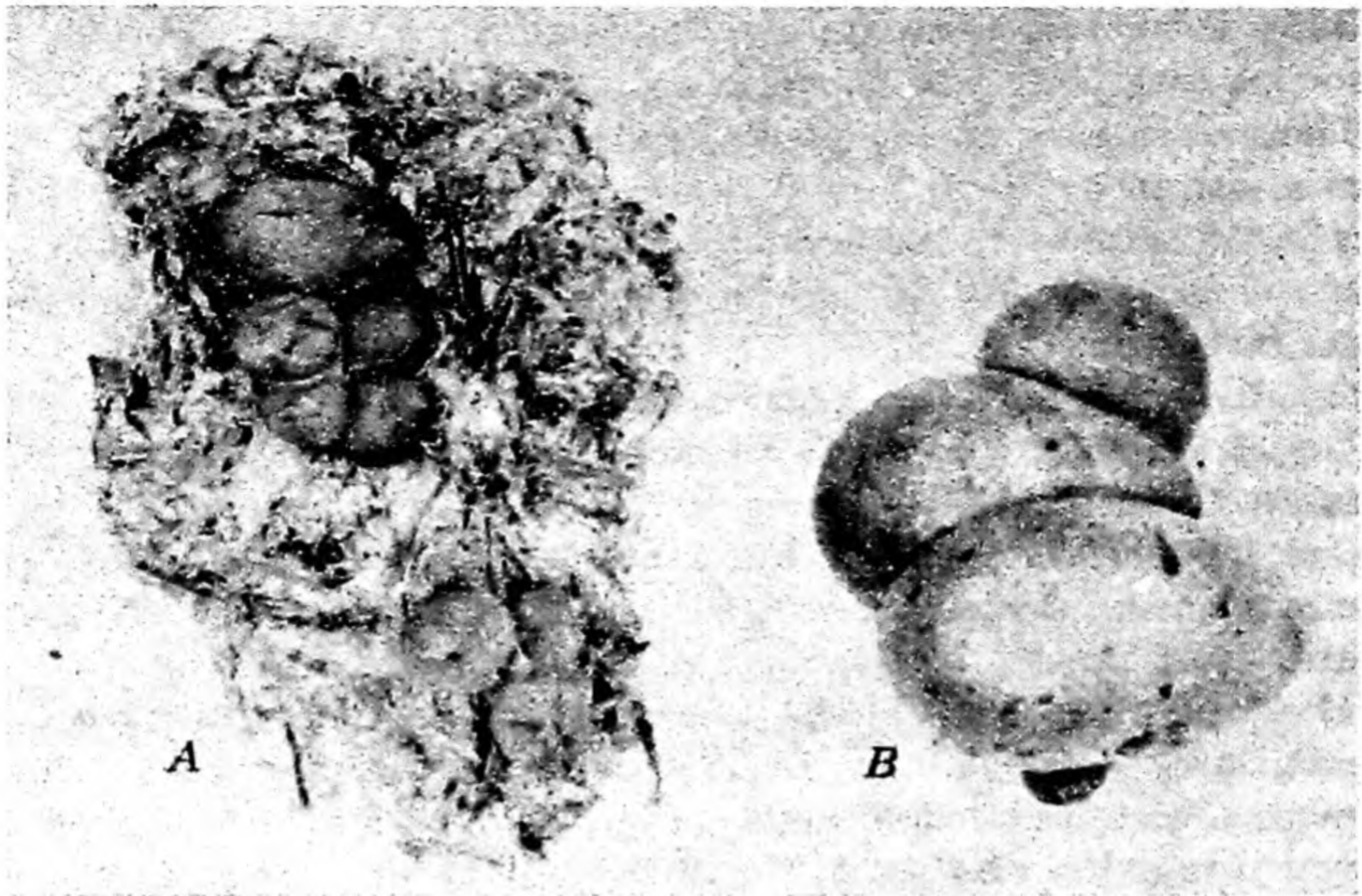


Figure 35. Aethalia. A. *Lycogala epidendrum*. B. *Lycogala flavofuscum*. Photograph by Philip G. Coleman.

There may also be a thin, cellophane-like base, the **hypothallus** (pl. **hypothalli**; Gr. *hypo* = under + *thallos* = shoot, thallus), from which the sporangia arise. Except for the hypothallus, which may serve as a common base for all sporangia, each of the latter is independent of all the others in the group. Examples of slime molds which produce sporangia are *Hemitrichia clavata*, *Physarum globuliferum*, *Physarum viride*, and various species of *Stemonitis*, *Comatricha*, and *Arcyria*.

The second type of fructification is called **aethalium** (pl. **aethalia**; Gr. *aethalos* = soot) (Figure 35). This is a fairly large, sometimes massive, generally cushion-shaped fructification which may represent a stage in the evolutionary development of the sporangia—a group of sporangia, so to speak, which have not separated into individual units.¹ In some aethalia the walls of the individual sporangia are quite evident; in others they are difficult to see; and in still others the aethalium shows no trace of sporangial walls. In all cases, the entire body is enclosed in a peridium which may or

¹ Another explanation is that the aethalium consists of several sporangia which have been fused into one structure during their evolutionary development, various degrees of fusion having been attained in different species.

may not be an aggregate structure. Some common examples of Myxomycetes whose fructifications are aethaloid are *Lycogala epidendrum* (Figure 35A), *Tubifera ferruginosa*, and various species of *Fuligo*.

The third type of fructification, the **plasmodiocarp** (*plasmodium* + Gr. *karpos* = fruit), is similar to a stalkless sporangium, but differs in that it retains, to a certain extent, the branching habit of the plasmodium. In the formation of the plasmodiocarp, the protoplasm concentrates around some of the main veins of the plasmodium and, secreting a membrane around itself, is converted into a fruiting structure which more or less retains the shape of the plasmodial venation at the time of fruiting. It is very difficult to draw the line between the sessile (stalkless) types of sporangia and short plasmodiocarps. These two forms actually merge into one another and are found side by side in the same group of fructifications, developed from a single plasmodium. In such mixed formations the plasmodiocarps are seldom branched. More often they are elongated, curved, or doughnut-shaped. An example of a truly plasmodiocarpous fructification is that of *Hemitrichia serpula* (Figure 36). A slime mold

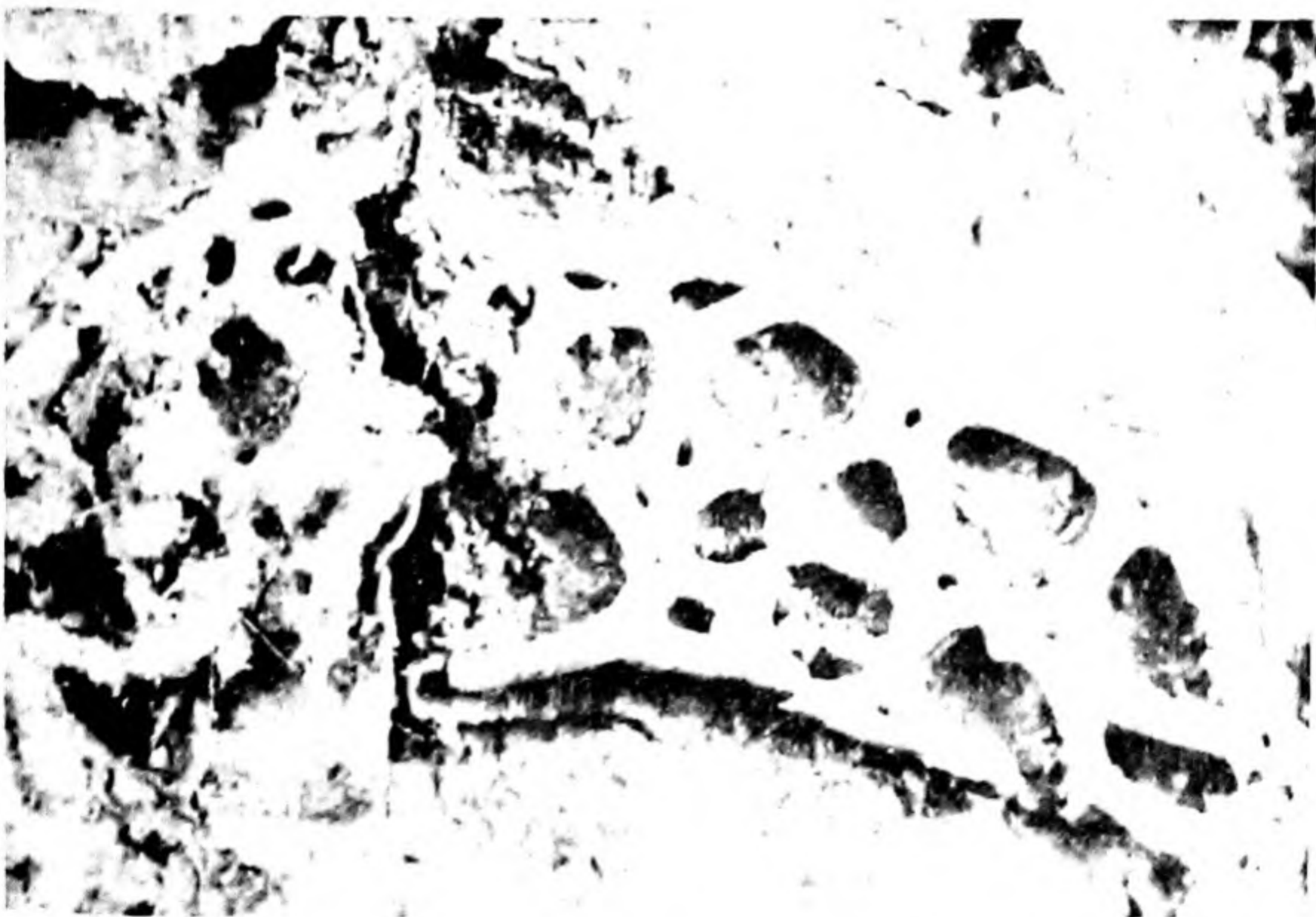


Figure 36. Plasmodiocarp of *Hemitrichia serpula*. Photograph by Philip G. Coleman.

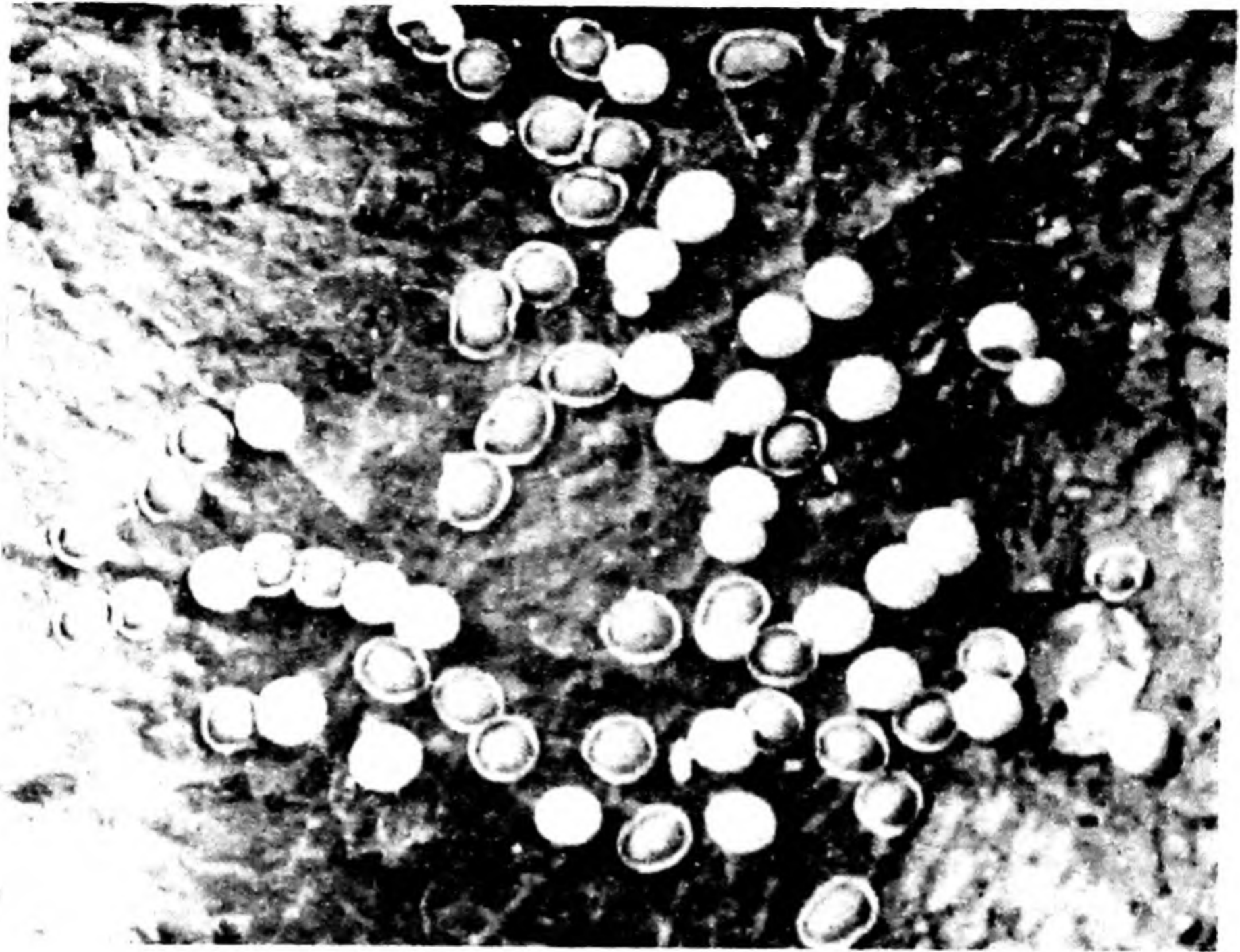


Figure 37. Sporangia of *Diderma testaceum*. Note the prominent columella in the broken sporangia. Photograph by Philip G. Coleman.

which often forms a mixture of sessile sporangia and plasmodiocarps is *Diderma testaceum* (Figure 37).

The type of fruiting body varies with the species and to some extent with environmental conditions prevailing during the development of the fructification. Light and moisture, for example, are known to influence the color of sporangia of *Physarum nutans*. When subjected to different degrees of humidity and light experimentally, plasmodia of this species formed gray, gray-green, or bright yellow sporangia (Brandza, 1926*b*). In some species, however, the color of the sporangia appears to remain constant under different environmental conditions.

The sporangial type of fructification may be stalked or sessile. Stalks, when present, vary in length, thickness, color, consistency, and structure, according to species. If the stalks extend into the sporangium, the intrasporangial portion is known as the **columella** (pl. *columellae*; L. *columen* = column). However, many species with stalkless sporangia also possess a columella (Figure 37).

The Capillitium. The presence and type of capillitium (pl. capillitia; L. *capillus* = hair) are important characteristics in the classification of the Myxomycetes. The capillitium is a group of non-living, hair-like structures which may be united to form an intricate network attached to the columella or to the peridium, or which may consist of simple or branched filaments, unattached and independent of each other (Figure 38).

In the Trichiales and Physarales (Harper and Dodge, 1914; Welden, 1955), when the sporangium is formed, but still immature, its protoplast becomes highly vacuolated. The vacuoles are probably formed by the liberation of water in which various materials are dissolved. These materials furnish the substances for capillitium formation within the vacuoles. The appearance of the vacuolar system at the initiation of capillitium formation corresponds closely to the appearance of the capillitium in a mature sporangium. Thus, if the capillitium is to be a network of filaments, the vacuolar system from which it will be formed develops into a tubular network; if the capillitium is to be composed of long threads, the vacuoles are elongated and possibly branched, but are scattered in the cytoplasm without coalescing. In the Physarales the capillitial material is deposited within the vacuoles, whereas in the Trichiales it is deposited on the surface of the vacuoles.

In the Stemonitales (Ross, 1957a; Goodwin, 1961) and the Echinosteliales (Alexopoulos, 1960) the capillitium either forms as an out-

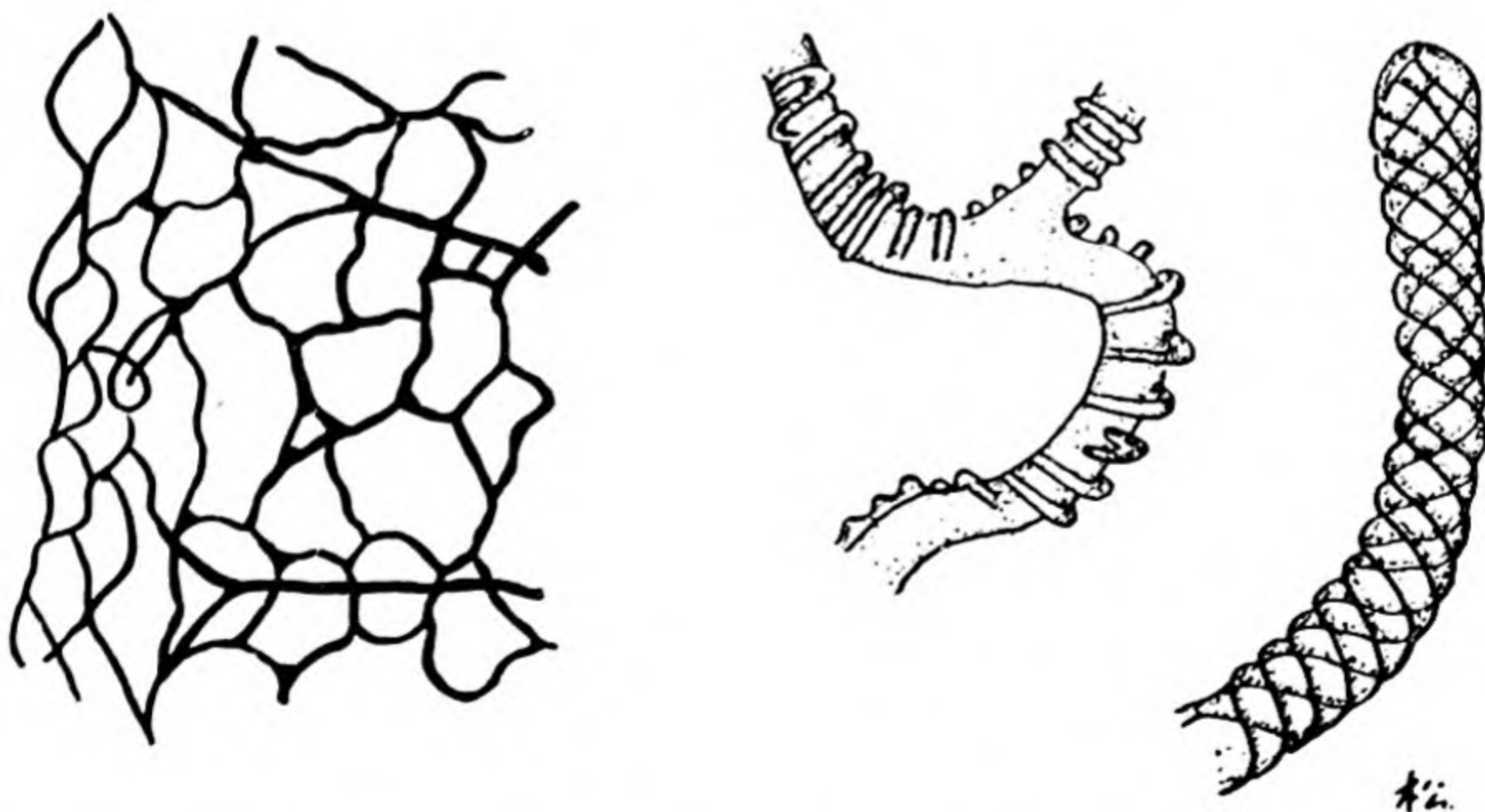


Figure 38. Three types of capillitium commonly found in Myxomycetes.

growth of the columella or is deposited in the cytoplasm without previous formation of a vacuolar system.

In many species the capillitium is an aid in the liberation of the spores. Forming a springy mat of threads, it expands when the peridium has disintegrated, and carries the spores with it to a considerable height above the base of the fructification. The spores are then easily dispersed from this position by air currents. *Arcyria nutans*, *Arcyria incarnata*, and *Hemitrichia vesparium* are good examples of slime molds with greatly expanding capillitia.

Spore Formation. Soon after the formation of capillitium, the numerous nuclei in the cytoplasm undergo division, which students of these organisms find to be meiotic (Wilson and Ross, 1957; Ross, 1961). Uninucleate portions of the protoplast are now separated from each other by the formation of a system of furrows, and a thick wall eventually envelops each spore. Thus, the entire protoplasm within the fructification is consumed in the development of the resting spores, which, in a mature fructification, occur closely packed in between the capillitial threads, but are in no way connected to them. The spores are loose within the fructification and are liberated upon the disintegration of the peridium.

order LICEALES

The spores of the Liceales are typically light in color. The fructifications, which may be of any one of the various types described, do not contain true capillitium, but may or may not contain **pseudocapillitium** (pl. **pseudocapillitia**; Gr. *pseudo* = false + *capillitium*). This is composed of irregular threads or plates representing remnants of plasmodial membranes or walls of fused sporangia rather than new elements formed at or immediately before spore formation. Martin (1949) lists three families and ten genera containing forty-three species. Some of the most common species are *Lycogala epidendrum* (Figure 35A), *Tubifera ferruginosa*, and *Dictydium cancellatum* (Figure 34B).

order TRICHIALES

The spores of the Trichiales are also light in color. This order differs from the Liceales in that the fructifications contain abundant capillitium. Two families and ten genera with a total of fifty-four species are listed by Martin. Representatives of the Trichiales are among the most ubiquitous of the Myxomycetes. The genera *Hemi*.



Figure 39. Sporangia of *Trichia scabra*. From Kodachrome transparency by the author.

trichia, *Trichia*, and *Arcyria* are well represented in the woods throughout the growing season. You can find *Hemitrichia clavata* on almost any fallen log that has retained some moisture, at almost any time from early spring to late fall. Other prevalent species of *Hemitrichia* are *Hemitrichia vesparium* and *Hemitrichia serpula*. *Trichia scabra* (Figure 39), *Trichia persimilis*, and *Trichia varia* are frequently collected. In the genus *Arcyria*, *Arcyria denudata*, *Arcyria incarnata*, *Arcyria nutans*, and *Arcyria cinerea* are commonly encountered.

order ECHINOSTELIALES

A small order with only four known species, the Echinosteliales contains the smallest of the Myxomycetes. The spores are colorless or lightly pigmented, rosy or golden yellow, and are characterized by thickenings in the wall at regular intervals. The peridium as a general rule disappears early in the formation of the fruiting body so that the mature sporangium is almost always naked. Capillitium is absent in two species, rudimentary in a third, and well developed into a tiny network in the fourth (Alexopoulos, 1961). *Echinostelium*

minutum develops abundantly on pieces of bark taken from living trees and placed in a moist chamber.

Three of the four known species have been induced to develop plasmodia in culture. All three formed protoplasmodia (Alexopoulos, 1960).

order STEMONITALES

This is the first order of the dark-spored Myxogastromycetidae. We have records of three families, twelve genera, and sixty-four species from North America. Lime is absent from the peridium and from the capillitium, but may be present on the stalk of the fructification. The capillitium is usually abundant, thread-like, and dark. *Stemonitis fusca*, *Stemonitis splendens*, and *Stemonitis axifera* are perhaps the most commonly found species in this genus. *Comatricha*

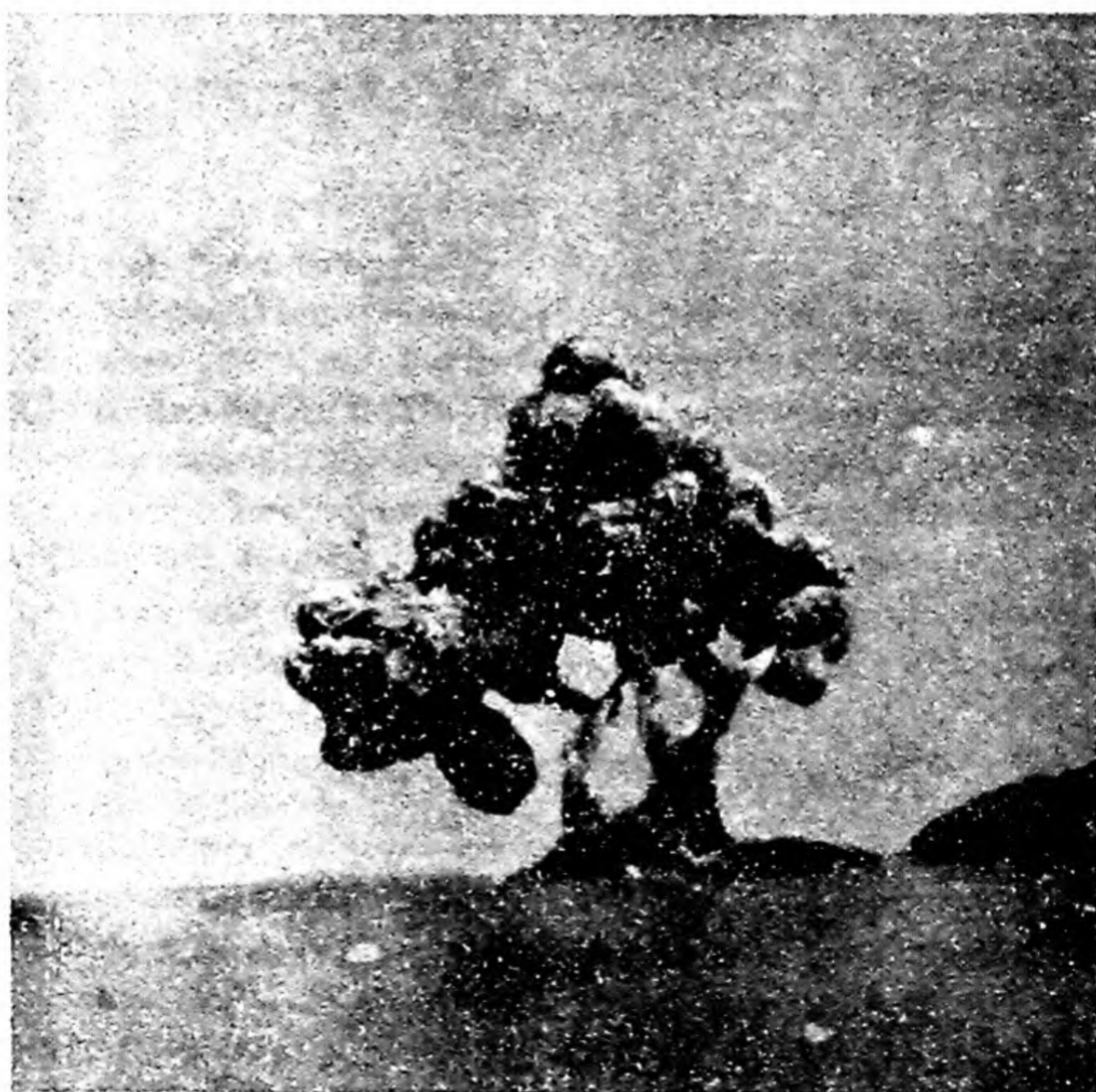


Figure 40. *Physarum nicaraguense*. Fruiting bodies developed in agar culture. Photograph by Fred W. Kent.

typhoides is one of the most prevalent species in the genus *Comatricha*. *Comatricha nigra*, *Comatricha laxa*, *Comatricha elegans*, and *Comatricha cornea* are minute species which develop their fructifications on pieces of bark taken from living trees and placed in a moist chamber. *Lamproderma arcyrioides* is a beautiful species with a golden-blue iridescent peridium.

order PHYSARALES

The last order of the Myxogastromycetidae is characterized by the usually abundant amount of lime present on the fructification. The order contains two families and twelve genera, with 142 species found on this continent. The genus *Physarum* with sixty-eight species is the largest. *Physarum polycephalum*, *Physarum viride*, *Physarum leucophaeum*, and *Physarum leucopodium* are some of the most widely distributed species. *Fuligo septica* forms large plasmodia and some of the largest aethalia in the Myxomycetes. It occurs on lawns, compost beds, and on growing plants over which the plasmodia creep in the summer. *Physarum nicaraguense* (Figure 40) is mostly tropical. *Badhamia*, *Diderma*, and *Didymium* are three other common genera in the Physarales.

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5 sub-division
EUMYCOTINA
the true fungi
class
CHYTRIDIOMYCETES
posteriorly uniflagellate fungi

Introduction. The sub-division Eumycotina contains all organisms, other than the slime molds, which we include in our current concept of fungi. What has been said in Chapter 1, therefore, refers more specifically to this group.

The Eumycotina consists of over 80,000 described species of true fungi. The great majority of fungi are filamentous organisms, their somatic thalli consisting of hyphae. A few of the primitive forms, however, are unicellular. All fungi have definite cell walls¹ and definite demonstrable nuclei, similar to those of higher forms of life.

How long fungi have inhabited the earth, or how they originated, are questions which have not been and may never be answered. Some fossil remains of fungi have been discovered, but studies of fossil fungi are so few and fragmentary that it is impossible to draw any definite conclusions as to the phylogeny of the group. At the present state of our knowledge, the origin of the fungi is entirely a matter of speculation. Some mycologists believe in a monophyletic origin from the green algae; others in a polyphyletic origin from various groups of algae; and still others in a monophyletic or polyphyletic protozoan ancestry. Opinions differ also concerning the evolution of the fungi. In general, botanists consider the aquatic

¹ In the small genus *Coelomomyces* of the Chytridiomycetes the mycelium is naked.

habitat more primitive than the terrestrial. In keeping with this principle, we consider fungi producing motile structures (zoöspores and planogametes) which depend on water for their function more primitive than those in which no motile structures are formed. Within a morphological series, parasites are considered more advanced than saprobes, obligate parasites more advanced than facultative ones, and highly specialized obligate parasites more advanced than less specialized species. In the development of fungal structures, the evolutionary curve which is thought to have taken place begins with simplicity, proceeds to complexity, and ends with degeneration and loss of structure.

Obviously it is impossible in an introductory course, for which this book is intended, to discuss all the fungi, or even representatives of all the groups. The examples chosen for discussion have been selected with the purpose of acquainting you with the basic structure of the fungi and of illustrating the evolutionary tendencies in this great group of organisms.

The sub-division Eumycotina consists of eight classes and one form-class. These are the Chytridiomycetes, Hyphochytridiomycetes, Plasmodiophoromycetes, Oömycetes, Zygomycetes, Trichomycetes, Ascomycetes, Basidiomycetes, and the Deuteromycetes.

The first six of the classes just listed, together with the Myxomycetes, are often referred to as the lower fungi. The majority of these produce their spores in sporangia. Many produce motile spores or motile gametes. As we proceed from the more primitive to the more advanced forms, and from an aquatic to a terrestrial habitat, we find a tendency for the sporangium to behave as a conidium, and eventually we reach the higher forms in which sporangia have given way completely to conidia. This transition will become apparent as you study the various forms in the discussions that follow.

The rest of this chapter deals with the class Chytridiomycetes.

General Characteristics. The one characteristic which distinguishes the Chytridiomycetes from all other fungi is the production of motile cells (zoöspores or planogametes), each with a single, posterior, whiplash flagellum (Sparrow, 1958/1959). Other characters which Chytridiomycetes have in common but which other fungi may also exhibit are (1) the coenocytic structure of the thallus, be it a multinucleate globose or oval structure, an elongated simple hypha, or a well-developed mycelium, and (2) the conversion of the zygote into a resting spore or a resting sporangium or, in one order, its growth into a diploid coenocytic thallus.

Mycologists who are interested in discovering relationships among

fungi are paying increasing attention to physiological and microchemical evidence to supplement morphological observations. The composition of the cell wall of fungi certainly is an important indication of relationships. From the evidence at hand it appears that chitin is the chief constituent of the cell walls of the Chytridiomycetes, but cellulose has also been reported from a number of species and is said in some forms to be masked by the chitin so that it is difficult to determine the presence of the cellulose. Research along these lines with modern methods of analysis will show how far-reaching are the relationships among the Chytridiomycetes now postulated almost entirely on the basis of morphological and life history data.

Occurrence, and Importance to Man. The Chytridiomycetes are typically found in aquatic habitats. Many of them, however, also inhabit the soil. Because of their microscopic size they cannot be observed in nature directly. They can be detected only by microscopic examination of the tissues of living plants which some of them parasitize or of dead organic material on which they grow, or in artificial culture in which a number of them form colonies of considerable size.

Students of these organisms have devised special methods for trapping, collecting, and culturing them in the laboratory on artificial media. In his authoritative book on the aquatic species of the lower fungi, Professor Sparrow of the University of Michigan, an eminent student of these fungi, has brought together (Sparrow, 1960) the important information we have on their collection and culture. Dr. Ralph Emerson of the University of California, who has also done much work on the lower fungi, has recorded (Emerson, 1958) his methods for culturing many of these organisms for laboratory instruction.

Most Chytridiomycetes are of little direct economic importance. Some parasitize and destroy algae which form a link in the food chain of aquatic animals. They are thus indirectly injurious to man. Members of the genera *Synchytrium* and *Physoderma* are parasitic on economic plants.

In relatively recent years, mycologists have found various species of *Allomyces*, and *Blastocladiella* to be valuable research tools in the study of morphogenesis. As such, these fungi are certainly of considerable importance to the welfare of man.

Somatic Structures. The most primitive Chytridiomycetes are unicellular and holocarpic. Such organisms have no mycelium and, in the early stages of their development, may lack cell walls. These

forms are sometimes separated into a distinct class, the Archimycetes (Gäumann and Dodge, 1928; Gäumann, 1952). In somewhat more advanced species, a few **rhizoids** (Gr. *rhiza* = root + *-oides* = like) are produced which serve to anchor the unicellular thallus to its substratum. Rhizoids are short, thin branches, superficially resembling a root system (Figure 43A). Some species produce a many-branched **rhizomycelium** (Gr. *rhiza* = root + *mycelium*). This is an extensive system of hypha-like filaments which usually do not contain nuclei. In still more advanced forms, a scanty mycelium, represented only by a few short hyphal branches, is produced. The most advanced of the Chytridiomycetes have a true mycelial thallus. Although as previously mentioned, the hyphae of such species are typically coenocytic, a septum is regularly formed at the base of each reproductive organ. Such septa are solid plates. In addition, the mycelium of the higher Chytridiomycetes may form **pseudosepta** (Gr. *pseudo* = false). These are septum-like partitions or plugs of a chemical composition different from that of the hyphal walls, which are deposited at intervals in the hyphae.

Asexual Reproduction. As it is in the majority of the lower fungi, the sporangium is the asexual reproductive structure of the Chytridiomycetes. In the young stage, sporangia are full of protoplasm containing many nuclei. As the sporangium develops, the entire protoplast undergoes cleavage into numerous, minute sections each of which develops into a uninucleate zoospore. After discharge, the zoospore swims for a time, encysts, withdrawing or losing its flagellum in the process, and then germinates, usually after a short rest period.

Sexual Reproduction. Sexual reproduction in the Chytridiomycetes is accomplished by one of the following methods.

1. **Planogametic Copulation.** a. *Conjugation of isogamous planogametes.* The two gametes are morphologically similar, but physiologically different. They unite in water to form a motile zygote. In some species, gametes originating in the same gametangium will not copulate. Examples of fungi which produce isogamous planogametes are *Olpidium viciae* and *Synchytrium endobioticum*.

b. *Conjugation of anisogamous planogametes.* One planogamete is considerably larger than the other. Copulation takes place in water, and a motile zygote is formed. This type of sexual reproduction is found only in some species in the order Blastocladales.

c. *Fertilization of a non-motile female gamete (egg) by a motile male gamete (antherozoid).* The male, motile gametes are released

from the male gametangia (antheridia) into the water and swim away. Some of them reach the female gametangia (oögonia), whereupon one antherozoid enters each oögonium and unites with the egg within. This type of reproduction is found only in the order Monoblepharidales.

2. *Gametangial Copulation.* In the Chytridiomycetes this is accomplished by the transfer of the entire protoplast of one gametangium into the other.

3. *Somatogamy.* Fusion between rhizomycelial filaments is said to precede resting spore formation in some species of Chytridiomycetes, but this has not been confirmed.

Classification. The Chytridiomycetes are classified into three orders on the basis of their somatic and reproductive structures. In the order of their probable phylogenetic priority, they are the Chytridiales, the Blastocladales, and the Monoblepharidales.

SIMPLE KEY TO THE ORDERS OF THE CLASS CHYTRIDIOMYCETES

- | | |
|---|--------------------------|
| A. True mycelium lacking; rhizomycelium present in some species | <i>Chytridiales</i> |
| AA. True mycelium present | |
| B. Sexual reproduction by fusion of planogametes; thick-walled, resistant sporangia characteristically formed | <i>Blastocladales</i> |
| BB. Sexual reproduction by fusion of a male planogamete with a female aplanogamete; no resistant sporangia formed | <i>Monoblepharidales</i> |

order CHYTRIDIALES

The organisms included in this order, often referred to as chytrids, are water- or soil-inhabiting species, many of the former parasitic on algae and water molds, many of the latter on vascular plants. There are only a few economically serious parasites in the entire order. *Synchytrium endobioticum* causes the disease known as potato wart, which is widely distributed in the potato-growing regions of the world. This fungus causes hypertrophy and hyperplasia of the surface cell layers of the infected potato tubers, converting the latter into unsightly and useless masses of warty tissue. *Physoderma zeae-maydis* causes *Physoderma* brown spot of corn. *Urophlyctis alfalfae* causes crown wart of alfalfa, which sometimes results in serious de-

struction of the crop. Many of the Chytridiales are saprobic and have been cultured on artificial media by special methods.

General Characteristics. The most primitive Chytridiales are **endobiotic** (Gr. *endos* = within + *bios* = life), living entirely within the cells of their hosts. The mature thallus is surrounded by a cell wall, although the early stages may be naked. More advanced forms are **epibiotic** (Gr. *epi* = upon + *bios* = life), producing their reproductive organs on the surface of the host although their somatic structures may be sunken into the host tissues. There is considerable variation within the group in the structure of the thallus and the reproductive organs. Primitive species are holocarpic, whereas the more advanced species are eucarpic. In the eucarpic forms a system of rhizoids is an integral part of the thallus. This system of rhizoids, which is the soma of the fungus as distinguished from the reproductive organs which it bears, may be very limited and inconspicuous or may be well developed. It serves to anchor the organism on its substratum and to absorb food. If the rhizoidal system bears but a single reproductive structure, the thallus is **monocentric** (Gr. *monos* = alone, single + *kentron* = center); if it bears more than one reproductive structure, it is **polycentric** (Gr. *poly* = many + *kentron* = center), for such reproductive structures do not arise in tufts from a single point, but are scattered on the thallus, and are interconnected by an often extensive rhizomycelium.

Asexual reproduction in the Chytridiales is by means of zoöspores which are borne in sporangia and are discharged through one or more papillae. A discharge papilla is formed on the wall of the sporangium or the tip of a tube issuing from it. Some species always form a well-defined circular cap at the tip of a discharge papilla. This is the **operculum** (pl. **opercula**; L. *operculum* = lid). The species which form opercula we designate as **operculate**. Most species do not form opercula but discharge their zoöspores through a pore in the wall of the sporangium or discharge tube formed when the discharge papilla dissolves away. We call such species **inoperculate**.

Sexual reproduction is accomplished by a variety of methods, some of which will be described in connection with the individual species whose life histories are discussed in the following sections. However, in the majority of species sexual reproduction has not been discovered. When sexual reproduction occurs the result is a thick-walled resting spore or resting sporangium. Many species, however, are said to form resting spores asexually. Either sexual reproduction does not occur in such species, or it has not been observed. The fact

that some resting spores which had been described as asexually formed were later shown to result from sexual reproduction (Willoughby, 1957) indicates that all reports of asexually formed resting spores should be carefully reinvestigated.

The order Chytridiales is subdivided into several families, distinguished chiefly on the basis of sporangial form and development. The life histories of the Chytridiales vary to such a degree that no typical example could be selected as a general illustration. The four species discussed here—one from each of four families—will give you some idea of the diversity existing in this group and will illustrate different types of thalli, spore discharge mechanisms, and sexual reproduction.

family OLPIDIACEAE

The Olpidiaceae include holocarpic Chytridiales parasitic on algae, fungi, mosses, pollen grains, and flowering plants. The thallus is converted into a single sporangium or resting sporangium; sexual reproduction is by copulation of isoplanogametes. There are several genera in this family, of which *Olpidium* is probably the best known.

Olpidium viciae (Figure 41), investigated by Shunsuke Kusano (1912), one of the foremost Japanese mycologists, is parasitic on the leaves and stems of *Vicia unijuga*. When the infected parts of the host are wet, the zoöspores escape from the zoösporangium through an exit tube. After a period of swarming, they encyst on the surface of the host (Figures 41A, B). Infection takes place through a minute pore dissolved in the host cell wall through which the protoplast of the parasite enters the host cell, leaving the cyst on the outside (Figure 41C). Within the host cell, the parasite becomes attached to the host nucleus, secretes a membrane around itself, and grows into a zoösporangium while its nuclei divide repeatedly. Zoöspores are soon formed which escape and repeat the asexual life cycle (Figure 41D).

The sexual phase is initiated when two zoöspores, behaving as planogametes, copulate (Figures 41E, F). Apparently, the swarm cells which issue from a zoösporangium may behave either as zoöspores or planogametes. The copulating planogametes most frequently originate in different sporangia, but sister planogametes as well have been observed to fuse. Copulation of two gametes results in a motile zygote (Figures 41G, H), but, according to Kusano, karyogamy is postponed for some time. The zygote infects a host cell in the same manner as does a zoöspore (Figure 41I), but develops

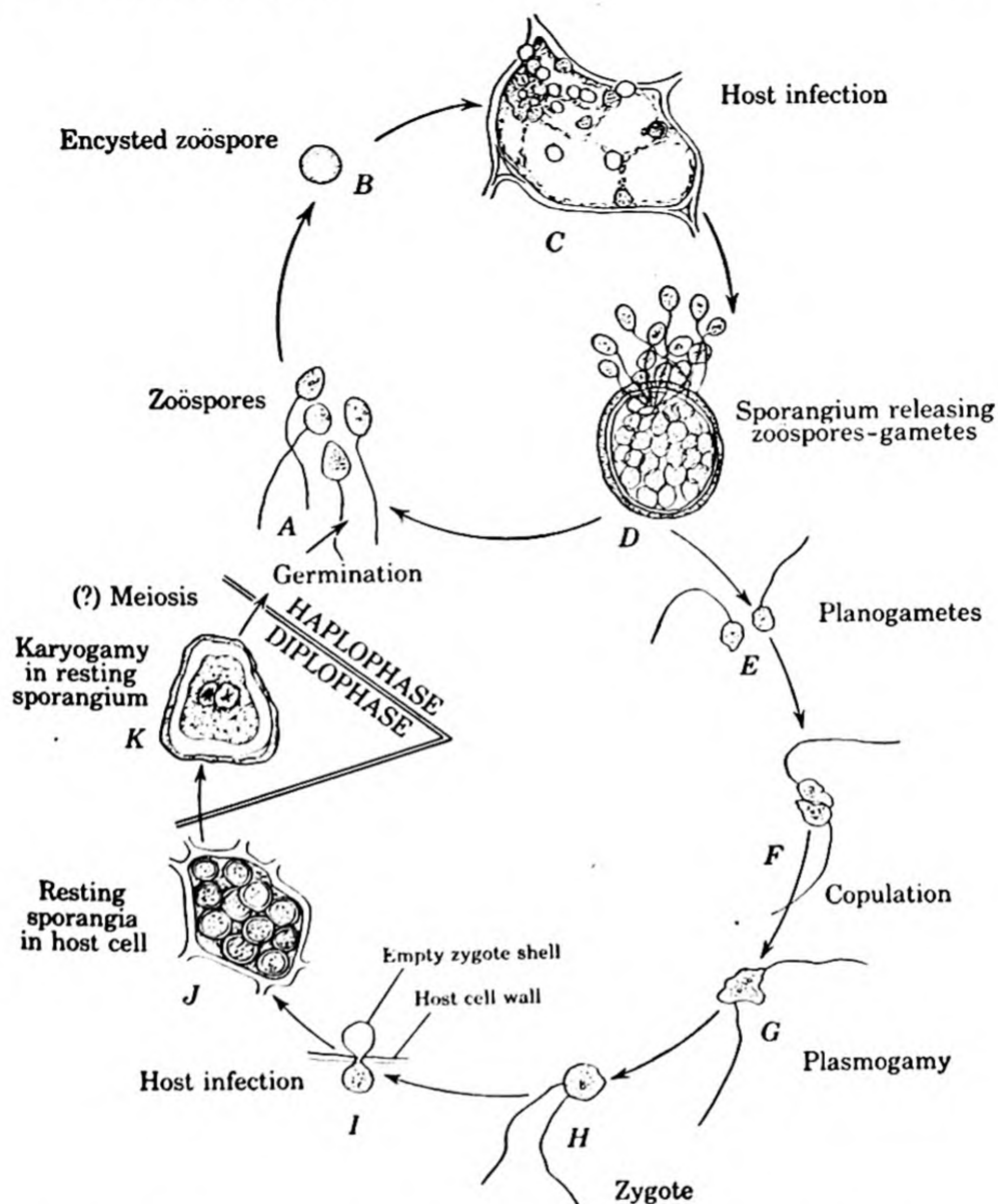


Figure 41. Life cycle of *Olpidium vioiae*. Redrawn from Kusano, 1912, *Jr. Coll. Agr. Tokyo Imp. Univ.*, 4:141-199.

into a thick-walled resting sporangium which is capable of overwintering (Figure 41J). The sporangium is binucleate at first, but, before germination, karyogamy takes place, probably followed by meiosis (Figure 41K). Several nuclear divisions result in a multinucleate structure the protoplast of which eventually undergoes

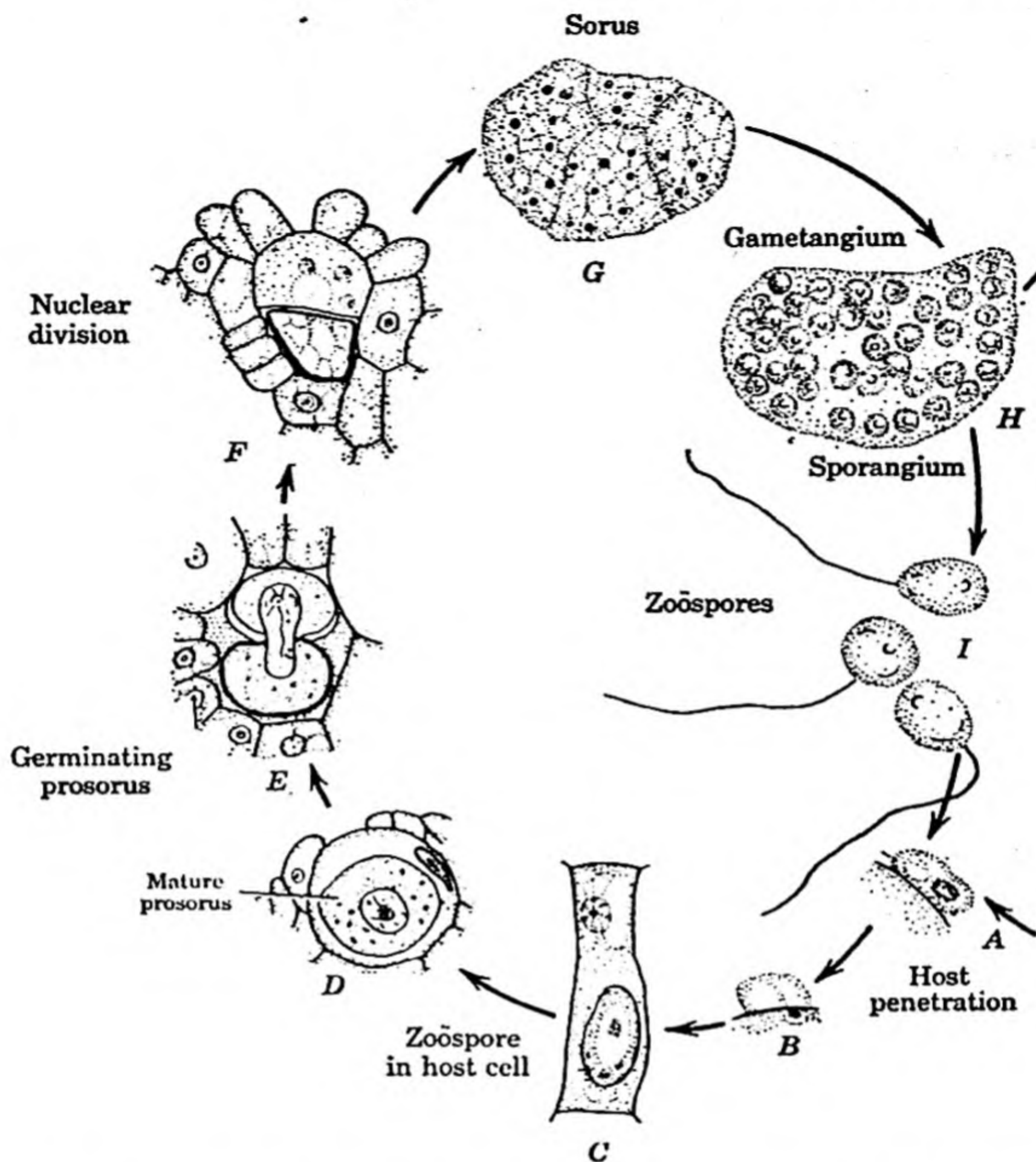


Figure 42. Life cycle of *Synchytrium endobioticum*. Redrawn by permission of the Royal Society of London, from Miss Curtis, 1921, *Phil. Trans. Roy. Soc. London*, B210:409-478.

cleavage into presumably uninucleate zoöspores. These escape and initiate a new life cycle.

family SYNCHYTRIACEAE

This is a family of parasitic, holocarpic Chytridiales in which the sporangia, as in the Olpidiaceae, are inoperculate. The thallus here, however, divides into several reproductive organs (sporangia or gametangia) which are enveloped in a common membrane and form a sorus. Sparrow (1960) recognizes three genera, of which *Synchy-*

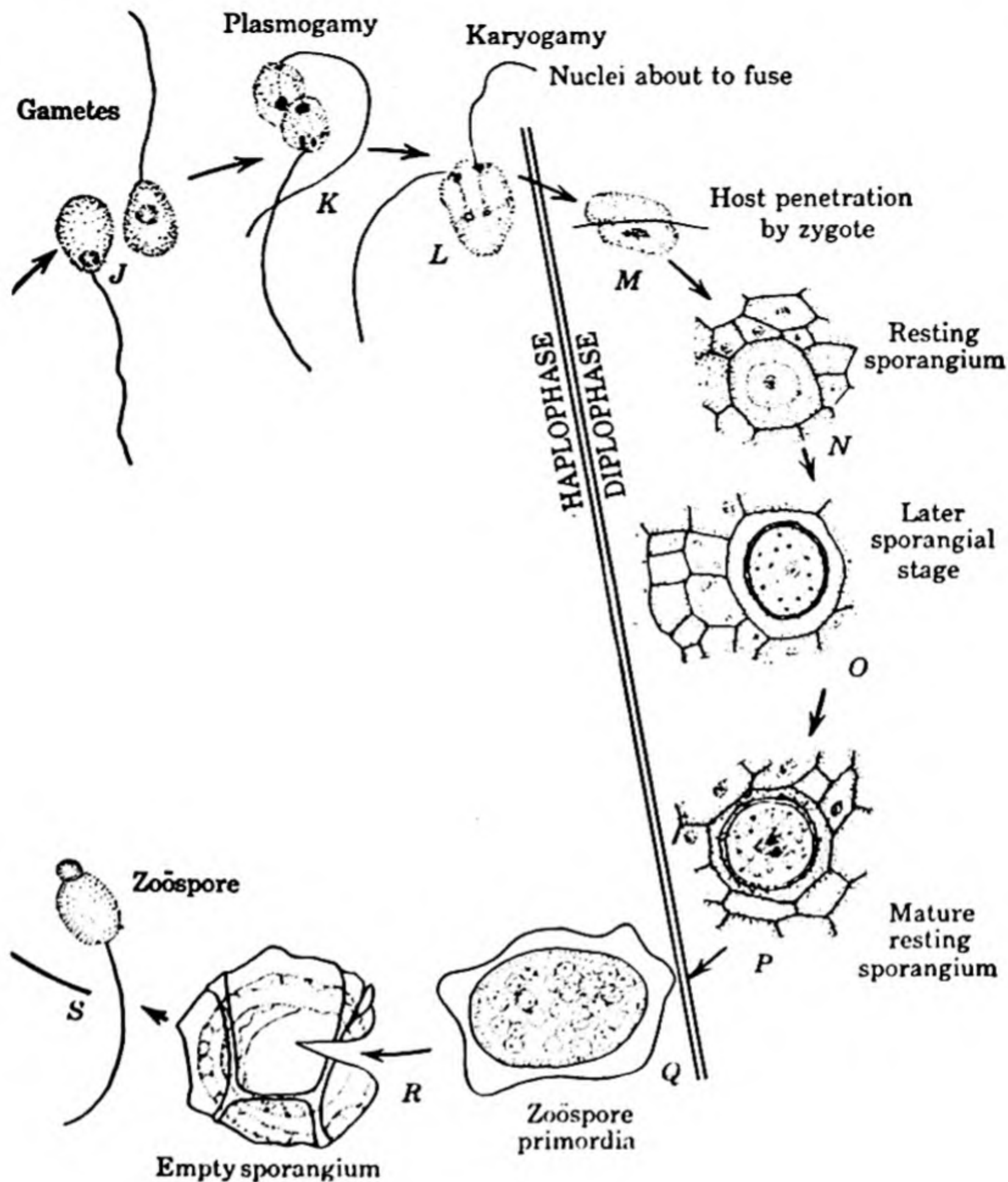


Figure 42 (Cont'd).

trium is by far the largest. Professor J. S. Karling of Purdue University, who has been studying this genus intensively for a number of years, subdivides it into seven sub-genera (Karling, 1955a). Unfortunately the life cycles of only a few of the 200 or so species of *Synchytrium* are known in detail. One of the best-known species is *Synchytrium endobioticum*, and a description of its life history, based on the excellent account given by Miss K. M. Curtis (1921), a British mycologist, will be described (Figure 42). As mentioned before, *Synchytrium endobioticum* is a serious parasite of potato tubers, causing black wart disease.

Infection of the potato tuber in the ground takes place in the spring when the zoöspores, released in great numbers from infected parts of plants, swim in a film of water present in the soil. Under suitable conditions, the uniflagellate zoöspore dissolves a minute pore in the epidermal wall of the host and penetrates, leaving its flagellum outside (Figures 42A, B, C). Once within the epidermal potato cell, the amoeboid spore sinks to the bottom of the cell or is carried there by protoplasmic streaming. Absorbing food from the surrounding protoplast, the parasite remains unicellular but grows in size, its nucleus becoming greatly enlarged. After reaching a certain size, it secretes a thick, golden-brown wall, and the structure is now the mature **prosorus** (pl. **prosori**; Gr. *pro* = before + *soros* = heap) (Figure 42D). Meanwhile, as the result of hypertrophy, the host cell has become greatly enlarged and pear-shaped. The surrounding epidermal and cortical cells have been stimulated to divide, forming a tumor or wart-like tissue from which the disease gets its name. The infected cell is in the center and is surrounded by a rosette of more or less hardened epidermal cells. The prosorus now occupies the lower half of the infected host cell, which, by this time, is dead.

Soon after maturing, the prosorus germinates within the host cell. Its wall ruptures, and the protoplast, surrounded by a very thin hyaline membrane, pushes out into the upper half of the host cell (Figure 42E). Repeated mitotic divisions of the nucleus (Figure 42F) now take place. The number of nuclei at this stage is in the neighborhood of thirty-two. A number of thin hyaline walls are now laid down in such a way as to divide the prosorus into from four to nine multinucleate segments (Figure 42G). Repeated nuclear divisions increase the number of nuclei in each of these segments until from 200 to 300 have been formed. Each prosoral portion thus develops into a sporangium or a gametangium, depending on the environment (Figure 42H). This mass of sporangia is the sorus. If water is abundantly present, zoöspores are formed. If, on the other hand, a period of drought sets in, the motile cells released are planogametes instead of zoöspores, and fuse in pairs to form zygotes. According to Miss Curtis, lack of water at a certain period in the development of the fungus affords a maturation period between formation and release which is necessary for the formation of gametes. If the motile cells are released immediately after their formation, they behave as zoöspores. In either case, the cell in which they are formed is the same, and may be called a zoösporangium or a gametangium, depending on the behavior of the motile cells released. Here then is one example of the physiology of a structure being controlled by the

environment. Whether the motile cells will be asexual zoöspores or sex cells (gametes) seems to depend on the presence or absence of sufficient water at a critical point in their development, and can be controlled at will by the experimenter, as Miss Curtis showed. In nature, more zoöspores are formed at the beginning than at the end of the season, and the reverse is true for gametes.

The entire protoplast of each sporangium becomes segmented into as many portions as there are nuclei, and each minute portion, consisting of a nucleus with its surrounding cytoplasm, develops into a uninucleate, uniflagellate zoöspore. When the zoöspores are mature, the sporangia are forced out of the sorus on the surface of the host. The zoöspores now escape in the presence of a film of water and initiate a series of new infections, thus completing the asexual phase of the life cycle. This phase may be repeated several times during the season (Figure 42I).

As mentioned above, under certain conditions the segments of the prosorus develop into gametangia. These are indistinguishable from zoösporangia except for the fact that they give rise to planogametes (Figure 42J), which are somewhat smaller than the zoöspores, and which copulate in pairs. It appears that planogametes originating in the same gametangium do not copulate, but that planogametes from different gametangia in the same sorus may fuse. There seems to be, therefore, a physiological differentiation between gametes in different gametangia. Copulation of gametes takes place in a film of water on the surface of the host or in the soil; karyogamy follows plasmogamy, and the biflagellate zygote swims about for some time before it finally comes to rest on the host (Figures 42K, L). The zygote now penetrates an epidermal cell in the same manner as described for the zoöspore (Figure 42M), and soon sinks to the bottom of the infected cell, which is stimulated to divide repeatedly. As a result of these divisions and of the pressures developed, the infected cell is buried rather deeply within the tissues. The parasite now enlarges, and the formation of a heavy wall around it converts it into a resting sporangium which remains dormant through the winter (Figures 42N-P).

The following spring a number of granules appear in the cytoplasm of the resting sporangium. These are the primordia of the zoöspores being formed. During zoöspore formation a large amount of chromatin is extruded from the primordial granules, and Miss Curtis concluded that, since she was unable to observe meiosis, this chromatin extrusion may be the equivalent of meiosis. However, in view of what happens in all other fungi whose cytology has been carefully

investigated it is probable that meiosis does occur at this point. The zoöspores which are liberated from the resting sporangium are larger than those released earlier in the life history from the zoösporangium, but function similarly (Figures 42Q-S).

Other species of *Synchytrium* which have been investigated in some detail are *Synchytrium fulgens* (Kusano, 1930) and *Synchytrium australe* (Karling, 1954; 1955c, d).

family PHLYCTIDIACEAE

The Phlyctidiaceae include about 100 species of eucarpic Chytridiales the thallus of which consists of a single cell (cyst) from which a haustorium or a group of rhizoids is developed. The cyst, which grows from a zoöspore, is converted into a zoösporangium or a gametangium. Sexual reproduction is by gametangial copulation, which results in the formation of a resting sporangium. *Rhizophidium*¹ is the largest of the eighteen genera included in this family by Sparrow (1960).

Rhizophidium couchii is one of the best-known species in this family. It is named after Dr. J. N. Couch of the University of North Carolina, an eminent student of the lower fungi, who first discovered this species. *Rhizophidium couchii* is parasitic on *Spirogyra*, a green alga which you have undoubtedly studied in general botany, and has been reported from the United States and from Europe on that host.

According to Couch (1932), the zoöspore settles on a *Spirogyra* filament and sends a rhizoidal process into the protoplast of the host through the wall (Figure 43A). The zoöspore, now in the form of a cyst, grows and develops into a sporangium in which a number of zoöspores are delimited. At maturity, a number of thin places develop in the wall and bulge out in the form of papillae because of internal pressure. Eventually the papillae burst and the spores emerge and swim away after first lingering near the mouth of the exit papilla (Figures 43B, C).

Sexual reproduction takes place by gametangial copulation. The female gametangium (oögonium) develops from a zoöspore in the same way as described for the sporangium except that no zoöspores are formed. A second zoöspore now attaches itself to the oögonium (Figure 43D). It does not enlarge, however, but remains small and behaves as an antheridium, emptying its contents into the oögonium through a pore or short fertilization tube (Figures 43E, F). After receiving the male protoplast, the oögonium develops into a thick-

¹ Also spelled *Rhizophydium*.

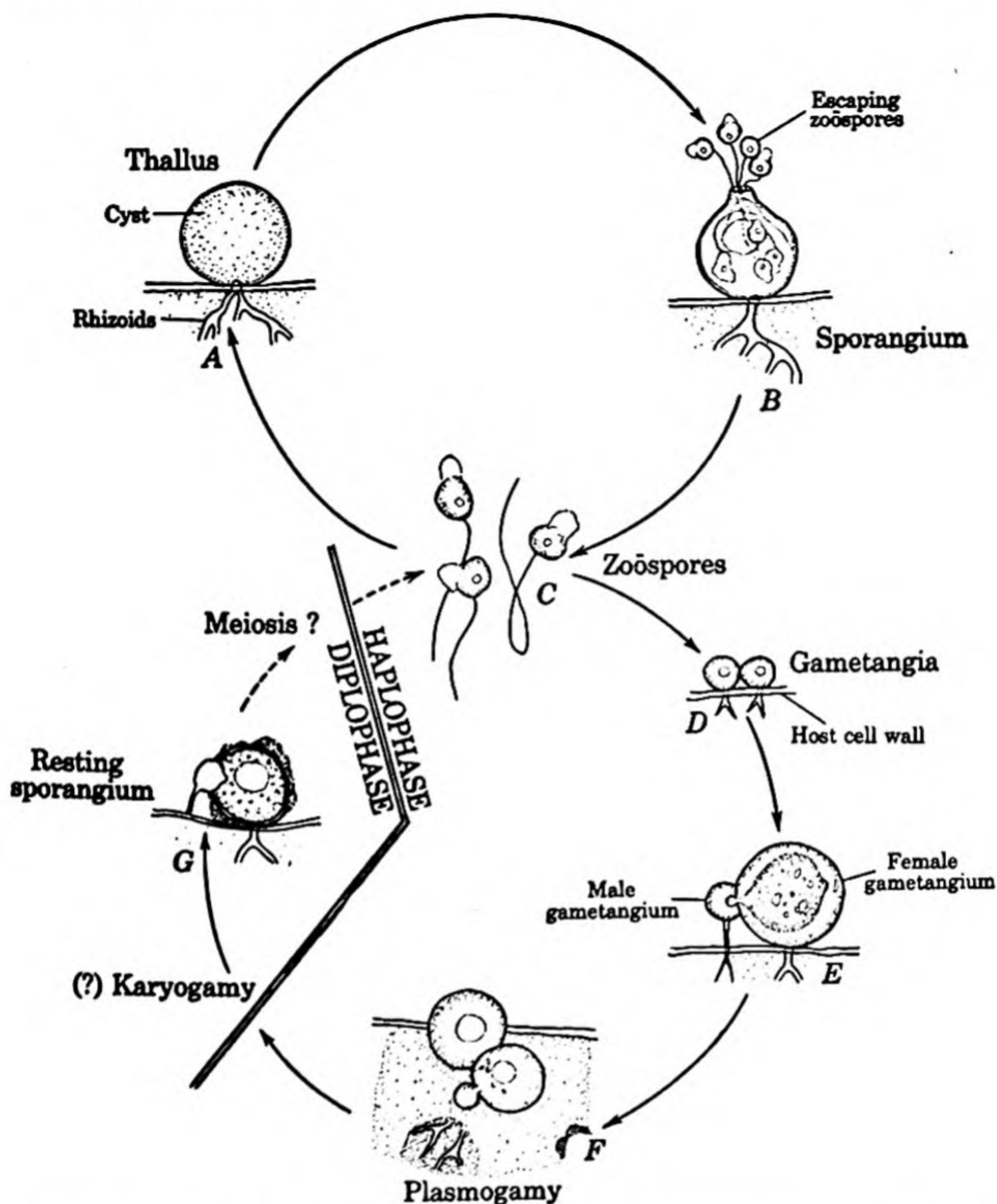


Figure 43. Life cycle of *Rhizophidium couchii*. A, constructed; B–G, redrawn from Sparrow, 1933, *Mycologia*, 25:513–535.

walled resting spore (Figure 43G). Sparrow (1933) found that in his material the two gametangia became initiated at about the same time as equal-sized zoospores, one enlarging, the other remaining small. Germination of the resting spore of an unidentified species closely resembling *Rhizophidium couchii*¹ takes place by the forma-

¹ Sparrow (1960) believes that it is probably the same species.

tion of a pore in the thick wall and the emergence of the protoplast, which develops into a sporangium. An apical exit papilla develops and deliquesces and the zoöspores escape (Karling, 1939).

family MEGACHYTRIACEAE

This is a relatively small family which includes three genera of operculate, polycentric Chytridiales. There are eleven species altogether, all of them aquatic saprobes living on decaying plant materials.

Nowakowskiella ramosa, which will serve as our example of this type of chytrid, appears to be widely distributed. It was originally discovered in India in 1907 and has since been found in Europe, Africa, and North and South America. The fungus is saprobic, living in nature on plant debris.

The thallus consists of profuse, richly branched filaments which are occasionally septate (Karling, 1944) and which bear terminal or intercallary sporangia and resting spores.

The zoöspores are normally uniflagellate (Figure 44C), although spores with two, three, and four flagella have also been seen. A crescent-shaped nuclear cap, which surrounds a third or more of the centrally located nucleus, is a conspicuous characteristic of the zoöspore. The nuclear cap disappears when the zoöspore comes to rest before germination. The sessile zoöspore now germinates by a single germ tube (Figure 44D) which begins to branch dichotomously (Figure 44E). Soon a swelling is formed (Figure 44F). The nucleus may remain in the spore until a swelling occurs in the filament, and then divide, the daughter nuclei migrating into the swelling, or it may migrate into the germ tube which then swells around the nucleus. As the thallus continues to grow, it branches dichotomously and produces more swellings. These are globose, spindle-shaped, or irregular in shape. According to Roberts (1948), no cross-walls are formed in the extensions of the thallus. Many-branched rhizoids, arising from various parts of the thallus, penetrate into the substratum and may expand into bladder-like structures. The nuclei are confined to the swellings. Neither the isthmuses which connect the swellings nor the rhizoids possess nuclei.

After the thallus has grown to some extent in the manner described above, filaments arise from the swellings or the isthmuses connecting them. These filaments, which Roberts calls flexuous filaments, branch repeatedly in a dichotomous manner and eventually form elongate,

spindle-shaped swellings in which many nuclei may usually be seen. Roberts believes that the flexuous filaments themselves are nucleated.

Zoösporangia are now formed from the swellings of the flexuous filaments. These are terminal or intercallary. As the swelling in-

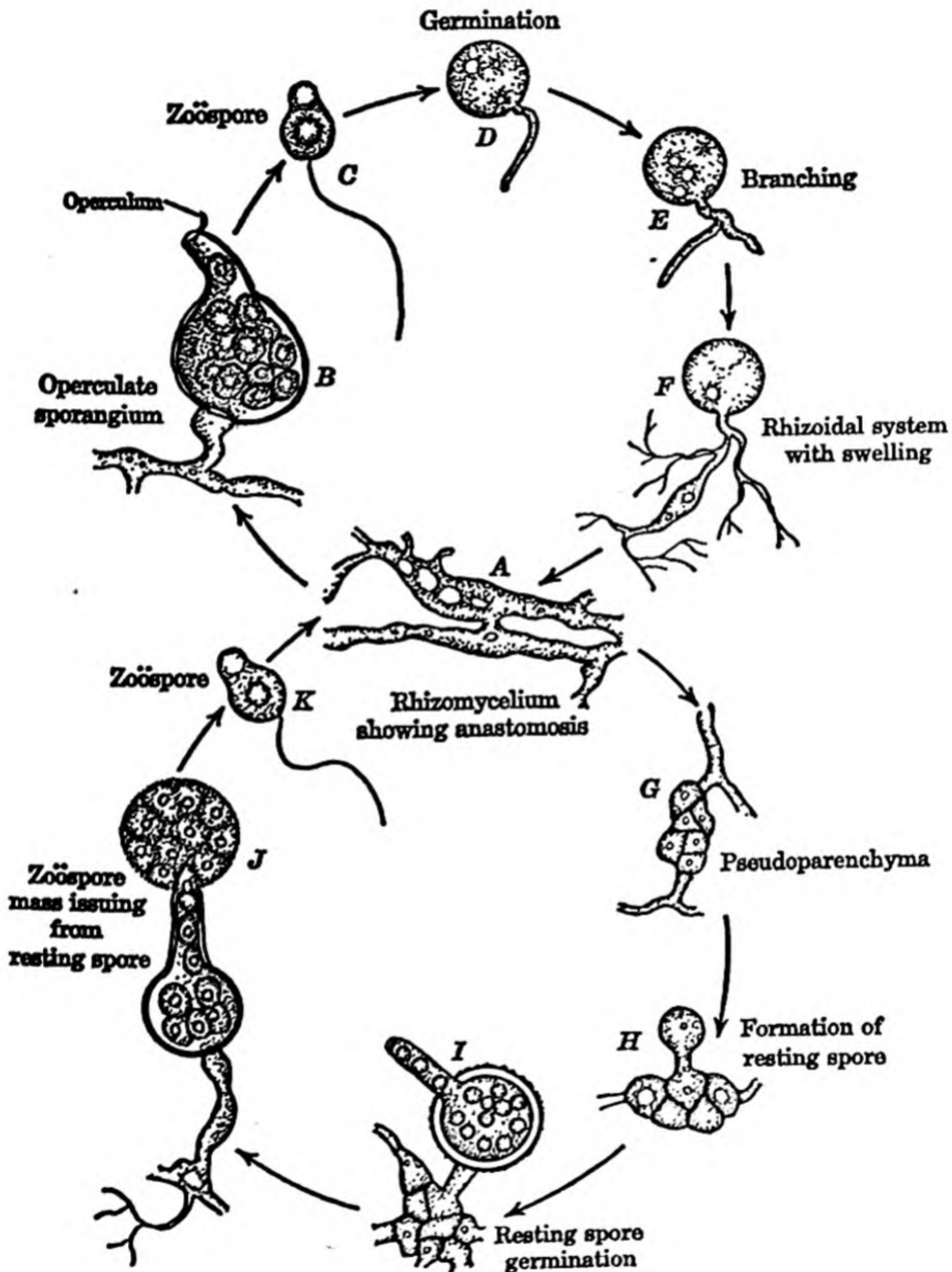


Figure 44. Life cycle of *Nowakowskietella ramosa*. Redrawn from Karling, 1944, *Bull. Torrey Bot. Club*, 71:374-389.

creases in size and becomes globose, a septum is formed at its base. Elongated, narrow vacuoles appearing in the cytoplasm cleave the contents of the zoösporangium into uninucleate portions which develop into zoöspores. The wall now thickens, and an operculum forms in the shape of an arched dome at the tip of the sporangium. The wall remains thin at the point of its attachment to the operculum.

At the time of germination, the operculum dehisces and is either forced off the sporangium or is turned back by internal pressure as if it were on a hinge (Figure 44B). The zoöspores escape individually. Anywhere from four to about forty zoöspores may be formed in each sporangium. The average number has been determined by Roberts as about thirty-six.

The resting spores or resting sporangia of *Nowakowskiella ramosa* develop from pseudoparenchymatous tissue (Figure 44G), which is formed in various ways. Several observers have described a fusion of cells which initiates the formation of the pseudoparenchyma, but no one has observed karyogamy, so that the significance of this fusion is not clear. The resting sporangia are therefore said to develop asexually, but the nuclear behavior which precedes their formation needs further investigation. Resting bodies either germinate directly by releasing zoöspores (Figure 44J), and thus behave as resting sporangia, or produce a thin-walled sporangium which releases zoöspores.

Nowakowskiella ramosa may be cultivated in the laboratory on cellophane in sterilized river water. The optimum temperature for its development appears to be 16–18° C.

You have now studied the life histories of four of the chytrids. The first two are holocarpic and live inside the host, passing their entire life cycle within a single host cell. They represent the most primitive fungi known. Their soma is unicellular—no mycelium; the zoösporangium is a simple structure which develops directly from the zoöspore. In one case (*Olpidium*) a single sporangium is formed from each zoöspore; in the other (*Synchytrium*) a whole sorus of sporangia is developed. Sexual reproduction is by copulation of isoplangametes released in water. This is the most primitive method of sexual reproduction known. What is more, the behavior of the swarm cells as zoöspores or gametes appears to be determined by the environment, and sex is not the definite phenomenon that it is in higher organisms. A resting sporangium is formed in both species as a result of sexual reproduction.

In the next example (*Rhizophidium*) you should note certain important differences. The thallus is eucarpic. It develops rhizoids

which constitute the somatic phase of the fungus and which do not develop into any other structure. They anchor the organism to the host and probably act as absorbing organs. The parasite is enabled to reproduce outside the host, sending only rhizoids into the host cells instead of being entirely immersed. This is the beginning of differentiation. Rhizoids are not hyphae, but a primitive type of soma. The sporangium still develops directly from the zoöspore. Sexual reproduction, however, is more advanced than in *Olpidium* or *Synchytrium*. Instead of motile gametes being released in the water and left to unite by chance, two gametangia contact each other and one sheds its contents into the other, sometimes through an especially developed fertilization tube. A resting structure again develops as a result of fertilization. This method of fertilization is sometimes called oögamous or oömycetous, one of the gametes being non-motile, acting as an egg, the other flowing through the pore or tube and fusing with the egg. Note that in none of these three fungi has meiosis actually been observed. Fungal chromosomes are very difficult to study because of their minute size.

In *Nowakowskiella*, the fourth chytrid studied, the thallus is not only eucarpic but also extensively developed. Of interest is the apparent differentiation of the rhizomycelium into a somatic and a reproductive phase. Karling (1944) does not mention it, but Roberts (1948) makes a considerable point of this situation. Another interesting development is the presence of nuclei in the flexuous filaments of the "reproductive phase" of the thallus. Such filaments certainly approach the structure of hyphae. Whether they are of significance in the evolutionary origin of fungal mycelium we cannot say. Sometimes superficial resemblances lead to erroneous conclusions. The presence of an operculum in the zoösporangia of *Nowakowskiella* should not go unnoticed. This is certainly a distinct structure which indicates some differentiation in the reproductive organ. No strong evidence can be presented at this time in favor of the existence of sexual reproduction in *Nowakowskiella*. Fusion of cells, however, is undeniable. This may indicate that at least a parasexual cycle is in operation. We have much to learn about the chytrids!

order BLASTOCLADIALES

The Blastocladales are chiefly water molds or soil inhabitants, characterized by the production of thick-walled, resistant sporangia, usually with pitted walls. Another feature which links the members

of this order is a prominent structure, the nuclear cap, located near the center of the zoöspore or planogamete. The characters of the thallus, of the sporangia, and of the sex organs, where known, vary greatly and can be discussed only in connection with individual groups. Three families are now recognized: Coelomomycetaceae, Catenariaceae, and Blastocladiaceae. Of these, the last is the best known.

The Coelomomycetaceae are obligately parasitic in the body cavities of mosquito larvae. They are of particular interest mycologically because their hyphae are naked, and somewhat resemble the strands of a myxomycete plasmodium. The entire mycelium is converted into thick-walled resistant sporangia which germinate, releasing a mass of zoöspores. Sexual reproduction is unknown in this family (Couch, 1945*b*; Couch and Dodge, 1947).

The Catenariaceae are a small family of parasitic or saprobic fungi. Some species are parasitic on microscopic animals, others on fungi; some are saprobic on plant and animal debris. The thallus is tubular, walled, and septate. It bears numerous rhizoids. The Catenariaceae reproduce both asexually and sexually. Sexual reproduction is by means of isogamous planogametes (Couch, 1945*a*).

family BLASTOCLADIACEAE

The soma of the Blastocladiaceae is well developed, usually consisting of (1) a group of well-formed, branched rhizoids by means of which the fungus attaches itself to the substratum; (2) a stout or slender trunk-like body; and (3) numerous side branches, usually dichotomously branched, on which the reproductive organs are formed. In some species, the thallus is simple rather than branched. The walls of the hyphae give a chitin reaction. The hyphae are non-septate, but pseudosepta, in the form of thickened rings, are present in some species.

In species known to reproduce sexually, two types of thalli are produced: gametothalli (haploid thalli) and sporothalli (diploid thalli). These two types, however, are distinguishable only by the types of reproductive organs they bear; the gametothalli normally produce gametangia, the sporothalli sporangia.

Sexual reproduction takes place by planogametic copulation. The copulating swimmers are either isogametes or anisogametes, depending on the species.

The Blastocladiaceae are subdivided into four genera of which *Allomyces* and *Blastocladiella* are the best known.

genus *ALLOMYCES*

Chiefly because of the early work of Hans Kniep, followed by the researches of Winslow Hatch, Ralph Emerson, Charles Wilson, Leonard Machlis, Gilbert Turian, and others, we now possess a great deal of information on the life cycles, cytology, genetics, and physiology of at least some members of this interesting genus, first discovered in India in 1911 by E. J. Butler, the distinguished British mycologist, and subsequently found to be widely distributed over the globe.

Three types of life cycle have been discovered in *Allomyces*, and on that basis Emerson (1941) established three sub-genera: *Euallomyces*, *Cystogenes*, and *Brachyallomyces*. The following discussion refers to *Euallomyces* (Figure 45).

Species of the sub-genus *Euallomyces* exhibit a definite alternation of generations, haploid gametothalli (Figures 45A, B) alternating with diploid sporothalli (Figure 45I). The two types of thalli are indistinguishable until they begin to form reproductive organs. The well-developed hyphae are dichotomously branched. Their walls consist chiefly of chitin, glucan, and ash (Aronson and Machlis, 1959). Gametothalli and sporothalli of the same strain have the same general nutritional requirements (Machlis and Crasemann, 1956). When they reach a certain stage of maturity, the gametothalli produce colorless female gametangia and orange male gametangia in close proximity to one another (Figure 45B) and usually in a 1:1 ratio. The orange pigment is in the cytoplasm which eventually becomes differentiated into male gametes, and is due to γ -carotene synthesized by the fungus (Emerson and Fox, 1940). The male gametangia are noticeably smaller than the female and may be borne on the latter (*Allomyces macrogynus*) or below them (*Allomyces arbuscula*). Both types of gametangia release motile gametes (planogametes) in the water. The gametes are posteriorly uniflagellate and of the same general structure as zoöspores typical of the Blastocladales in general (Figure 45C, D). Each exhibits, as do the zoöspores, a prominent nuclear cap consisting chiefly of RNA¹ (Turian, 1955, 1957). The male gametes are orange and about half the size of the female gametes.

Attracted by the sexual hormone sirenin (Gr. *seirin* = siren) produced by the female gametes (Machlis, 1958a, b), the male gametes copulate with the latter in pairs very soon after their release from

¹ Ribonucleic acid.

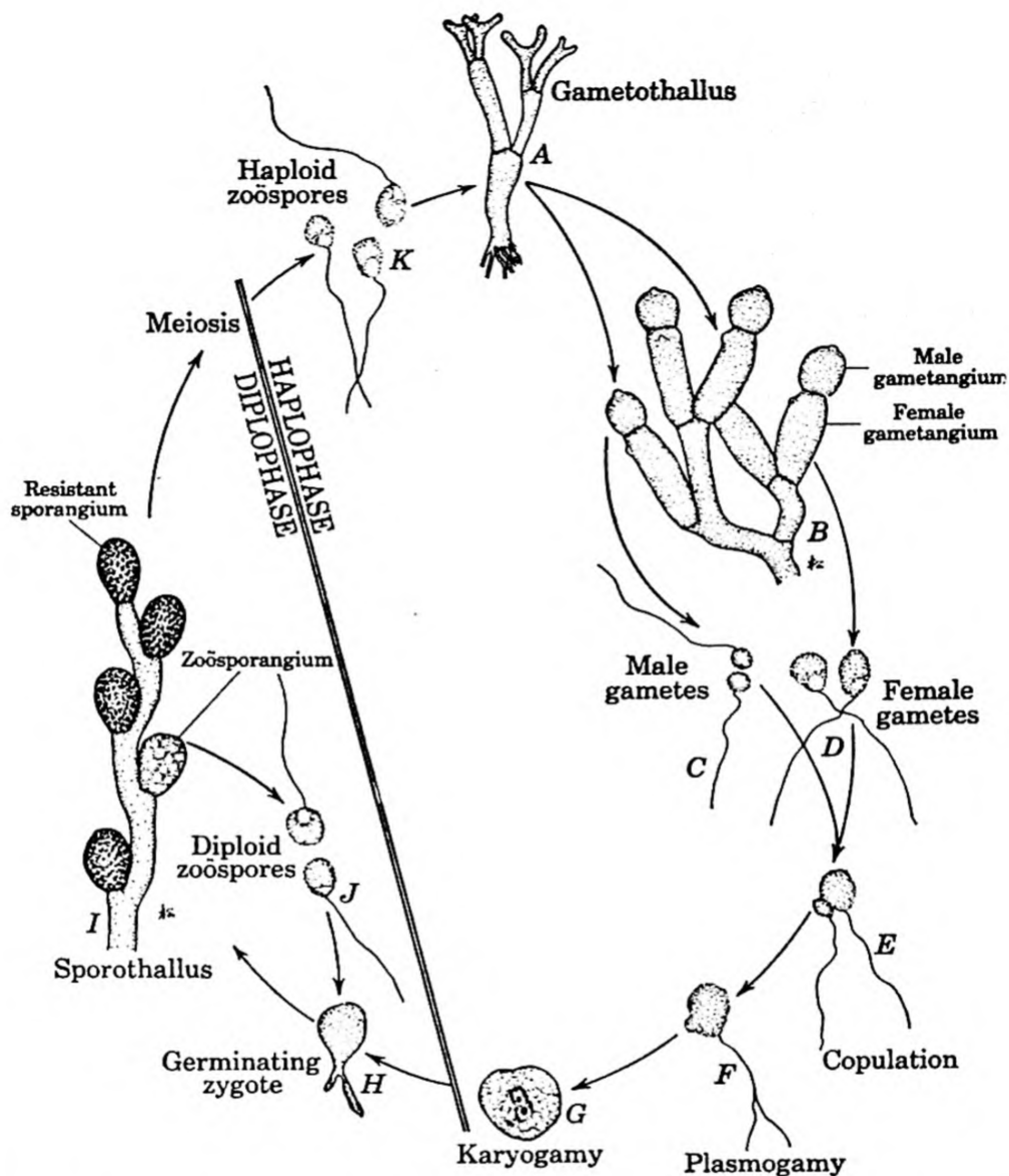


Figure 45. Life cycle of *Allomyces macrogynus*. A, H, redrawn from Emerson, 1941, *Lloydia*, 4:77-144; E, F, constructed; G, redrawn from Hatch, 1938, *Ann. Bot.*, n.s., 2:586-614.

the gametangia (Figure 45E). Copulation, however, may be completely prevented in culture by the addition of boric acid (dose of 1/15,000) to the water in which the gametothalli are growing (Turian, 1954). Karyogamy follows plasmogamy (Figures 45F, G), and the motile zygote comes to rest, loses its flagella, rounds up, and soon germinates. First a germ tube is produced which develops into rhizoids (Figure 45H). Then the main body of the zygote enlarges and gives rise to the first hyphal tube, which elongates, branches dichotomously, and develops into a diploid sporothallus (Figure 45I).

At maturity, the sporothalli form two types of sporangia: thin-walled, elongated, colorless zoösporangia (mitosporangia), and oval, thick-walled, pitted, resistant sporangia (meiosporangia) which contain melanin pigments (Emerson and Fox, 1940) and appear reddish brown (Figure 45I). The zoösporangia germinate soon after their formation, releasing diploid zoöspores (mitospores) which swim about for a time (Figure 45J), round up, and give rise to sporothalli, thus repeating the diploid generation. The resistant sporangia require a rest period of 2–8 weeks or more before they germinate, but Machlis and Ossia (1953) have been able to reduce the maturation period of certain strains of *Allomyces arbuscula* to as short a time as 2 days by changing the culture medium at the proper stage of development. Meiosis in the resistant sporangia takes place at the time of germination (Wilson, 1952) and results in the formation of haploid zoöspores (meiospores) (Figure 45K) which are slightly smaller than the diploid zoöspores. Upon germination, meiospores, being haploid, give rise to gametothalli, which produce gametangia instead of sporangia.

Cytological investigations (Emerson and Wilson, 1954; Wilson, 1952) which established that meiosis takes place in the resistant sporangia also revealed two general series of strains in *Euallomyces*. The basic haploid chromosome number in one series is 8. Strains with 16, 24, and 32 chromosomes have also been found, indicating that polyploidy has occurred. This is the *Allomyces arbuscula* series in which the male gametangia are hypogynous (located below the female). In the other series the basic chromosome number is 14, and strains have been found which appear to be polyploids with 28 and 56 (?) chromosomes. This is the *Allomyces macrogynus* series in which the male gametangia are epigynous (located terminally, above the female). Natural hybrids with other chromosome numbers have also been found.

Interspecific hybrids, different from both parent types, have been

obtained artificially (Emerson and Wilson, 1954). One interesting variation is represented by gametothalli which are nearly all (99+ per cent) female or nearly all male. Inasmuch as no sex chromosomes are involved here, sex determination is not genetically controlled—in the usual sense of the terms—and the explanation must be sought elsewhere. Turian (1960) induced female strains to revert partially to maleness by growing them on a synthetic medium with acetate as the single source of carbon and traces of coenzyme A, or with glucose as the carbon source enriched with glycine and folic acid. The same media induced a high degree of maleness (80–90 per cent) in a normally bisexual strain with a 1:1 male:female ratio. Thus we are approaching a physiological explanation for the morphological differentiation of sex in this fungus.

Another interesting result of genetic experiments was proof that *Allomyces javanicus*, originally discovered in Java and subsequently in several other widely separated localities, is a natural hybrid between *Allomyces arbuscula* and *Allomyces macrogynus*. By experimentally hybridizing these two species in the laboratory, Emerson and Wilson (1954) obtained *Allomyces javanicus*.

genus *BLASTOCLADIELLA*

This genus differs from *Allomyces* in that its thalli are minute, consisting in most species of a short unbranched hypha bearing a system of rhizoids at the lower end and a single reproductive organ at the tip. *Blastocladiella variabilis*, with a *Euallomyces* life cycle, consists of four types of thalli, each bearing a zoösporangium, a resistant sporangium, a male gametangium, or a female gametangium. The planogametes in this genus are isogamous. If you know the life cycle of *Euallomyces*, you should be able to construct an illustrated life cycle of *Blastocladiella variabilis*. Try it and then check your results with Figure 3 in Emerson's "The Biology of the Water Molds" (1955).

Blastocladiella emersonii, another species in this genus, has been studied intensively by Cantino and his associates. The organism consists of three kinds of morphologically distinct thalli bearing a thin-walled colorless sporangium, a thin-walled orange sporangium, or a thick-walled resistant sporangium. All sporangia produce posteriorly uniflagellate swarmers, the first two colorless ones, the last orange-colored. No one type of swarmer is capable of fusing with any other in the usual sense, but there is good reason to believe that cytoplasmic exchange may take place when a colorless swarmer and an orange swarmer of certain strains remain in contact for some time.

Cytoplasmic bridges temporarily formed between contacting swarmers have been observed (Cantino and Horenstein, 1954).

Studies on the morphogenesis of *Blastocladiella emersonii* have shown that CO_2 plays an important role in determining whether a sporeling will develop into a thallus bearing a resistant sporangium or a thallus bearing a zoösporangium. Essentially all sporelings exposed to NaHCO_3 develop into thalli bearing resistant sporangia, whereas ordinarily none does. Another important discovery (Cantino and Horenstein, 1956) concerned the effect of light on growth of *Blastocladiella emersonii*. It is now known that the organism grows better in light than in darkness and that the stimulatory effect involves increased CO_2 fixation under the influence of light. Further studies (Lovett and Cantino, 1960; Cantino, 1961a, b) are linking biochemical changes with morphological development so that little by little we are beginning to understand the physicochemical basis of structure in this fungus.

There are some important advancements which you should note in the Blastocladales. First of all, the thallus is now large enough to be seen with the unaided eye. This increase in size over the microscopic chytrids is in itself notable, for it permits considerable differentiation. The soma is now composed of true hyphae which carry on the metabolism of the fungus and form reproductive organs on their branches. No striking evolutionary advance is to be noted in the sporangia or zoöspores, except, of course, for the occurrence of diploid zoöspores which reproduce the sporothallus.

In sexual reproduction we find these fungi employing the primitive method of planogametic copulation which we observed in the simpler chytrids, but in *Allomyces* the planogametes have become unequal in size (anisogametes) and the two types are borne in separate, distinguishable gametangia. This differentiation represents an advancement over isoplanogametes and the method by which the latter are produced.

Another important fact is the lack of a sexual resting spore in this group. Its function has been taken over by the resistant sporangia. The definite alternation of generations that occurs in *Allomyces* and *Blastocladiella* is another interesting phenomenon that sets these fungi apart from all others.

order MONOBLEPHARIDALES

The Monoblepharidales, closely related to the Blastocladales, represent the culmination of the Chytridiomycetes. Only a few species are known, most of them aquatic. These are distributed

among the genera *Monoblepharis*, *Monoblepharella*, and *Gonapodya*. The first of these is placed in the family Monoblepharidaceae. The other two genera constitute the family Gonapodyaceae. Of no direct economic importance, these fungi are nevertheless of interest because of their method of sexual reproduction, found nowhere else among the fungi.

family MONOBLEPHARIDACEAE

Monoblepharis polymorpha Cornu

In *Monoblepharis polymorpha* (Figure 46) the somatic thallus consists of hyphae whose protoplasm, which is highly vacuolated, appears foamy (Figure 46A). This foamy appearance is characteristic of the entire order. The hyphae are well developed with many branches. Elongated sporangia are borne singly at the hyphal tips (Figure 46B). They are generally no larger in diameter than the somatic hyphae. The sporangia are subtended by a septum. Multinucleate from the first, the sporangial protoplast becomes divided into many uninucleate portions, each of which develops into a posteriorly uniflagellate zoospore (Figure 46C). The zoospores are released from the tip of the sporangium, swim for a time, become rounded, and germinate, each by a germ tube, forming a new mycelium.

The same thallus which produces the sporangia produces gametangia when subjected to higher temperatures. The gametangia are easily distinguishable as male and female, the narrow, elongated antheridia being borne on the rounded, larger oogonia (Figure 46D). A number of uniflagellate gametes, called antherozoids, are formed within and released from each antheridium (Figure 46E). The protoplast of the oogonium becomes rounded and forms a uninucleate oosphere (Gr. *oön* = egg + *sphaera* = sphere). An oosphere is defined by Fitzpatrick (1930) as "a single, large, spherical, naked, non-ciliate, and practically non-motile gamete."¹ This is the egg. In *Monoblepharis* it is uninucleate.

After the antherozoids (sperms) are released from the antheridia, they swim or creep over to the oogonia. A single sperm enters the oogonium through a papilla present in the oogonial wall, penetrates the oosphere, and fuses with it (plasmogamy) (Figures 46F, G). The fertilized egg soon emerges from the oogonium, and, while still attached to the oogonial wall by a hyaline collar, secretes a thick

¹ Quoted by permission of the McGraw-Hill Book Co., New York.

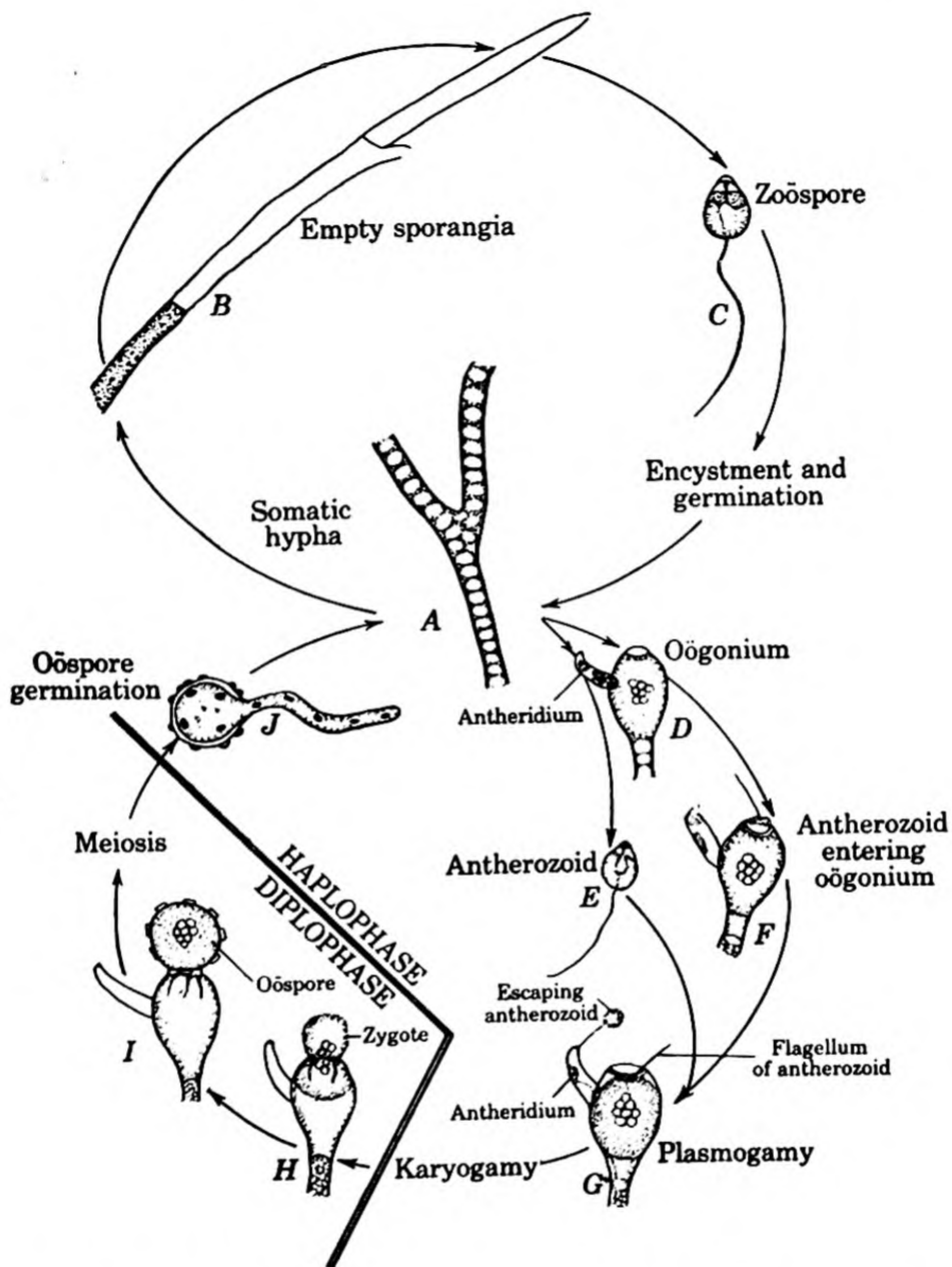


Figure 46. Life cycle of *Monoblepharis polymorpha*. C-I, redrawn from Sparrow, 1933, *Ann. Bot.*, 47:517-542; J, redrawn from Laibach, 1927, *Jahrb. wissen. Bot.*, 66:596-630.

wall around itself and develops into an oöspore (Gr. *oön* = egg + *sporos* = seed, spore) (Figures 46H, I). An oöspore is a thick-walled spore which develops from an oösphere either through fertilization or parthenogenesis (Gr. *parthenos* = virgin + *genesis* = birth). Karyogamy is delayed until the oöspore wall is partially formed. The oöspore germinates under favorable conditions by producing a hypha which develops into a new thallus (Figure 46J). Meiosis probably takes place during the germination of the oöspore, when the zygote nucleus first divides.

family GONAPODYACEAE

This family differs from the Monoblepharidaceae chiefly in the behavior of the zygote. In *Monoblepharella* fertilization of the oösphere occurs in the oögonium as in *Monoblepharis*, but the male gamete is only partially engulfed by the female, its flagellum remaining outside. The zygote now issues from the oögonium and swims free in the water, propelled by the flagellum of the antherozoid. In *Gonapodya* the female gametangium may form more than one gamete. The eggs are fertilized either within the oögonium or after being discharged. The zygotes behave as in *Monoblepharella*, using the flagellum of the antherozoid to propel themselves through the water. The oöspores develop a thick, smooth wall (Johns and Benjamin, 1954).

The following then are the important changes which have occurred in the Monoblepharidales from previous orders studied. The mycelial type of soma, which consists of well-developed hyphae, and which is characteristic of the vast majority of fungi, is now well established. The elongated hypha-like sporangium, characteristic of a great many water molds (see Chapter 7), is found here for the first time. Sexual reproduction as it occurs in the Monoblepharidales is found nowhere else in the fungous world. However, the important development in this order is the first appearance of the definite oösphere which, upon fertilization, develops into a definite oöspore. The oöspore germinates by germ tube instead of forming zoöspores as do the resting sporangia of the Chytridiales.

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⑥ class
HYPHOCHYTRIDIOMYCETES
order
HYPHOCHYTRIALES
anteriorly uniflagellate fungi

The Hyphochytridiomycetes are aquatic, freshwater or marine chytrid-like fungi whose motile cells are anteriorly uniflagellate, possessing a flagellum of the tinsel type. They are parasitic on algae and fungi or saprobic on plant and insect debris in the waters in which they live. All are included in the single order Hyphochytriales.

As compared to the Chytridiomycetes, the class Hyphochytridiomycetes is very small, consisting of about fifteen known species. There is, however, considerable variation among these fungi, reflected in their classification into six (or seven) genera which have been placed in three families: Anisopidiaceae, Rhizidiomycetaceae, and Hyphochytriaceae.

The resemblance of the Hyphochytriales to the chytrids is so great that for many years the few known species were included in the Chytridiales (Gäumann, 1952) in spite of the difference in the structure of the flagellum and its position on the zoospore. As more species were discovered, greater attention was paid to their classification, and it was eventually recognized that these fungi should be treated as a group separate from the Chytridiales.

The walls of all species which have been investigated contain chitin. In addition, cellulose is present in some (Nabel, 1939; Fuller and Barshad, 1960). The thallus, which may be holocarpic or eucarpic, shows an evolution which parallels that of the chytridiaceous thallus. In the holocarpic species the thallus is endobiotic and is converted into a zoosporangium. In the eucarpic forms the thallus may consist of a single reproductive organ bearing a branched

rhizoidal system, or may be polycentric and consist of branched hyphae with some septa.

The zoösporangia are inoperculate and release their zoöspores through discharge tubes. The zoöspores germinate and reproduce the thallus. Sexual reproduction is known only in the genus *Reessia* (Sparrow, 1960), whose systematic position is still uncertain and whose morphology requires reinvestigation.

Rhizidiomyces apophysatus, one of the better-known Hyphochytriales, will serve as our example of this small class of fungi. The following account is based on Karling's discussion (1944).

family RHIZIDIOMYCETACEAE

The Rhizidiomycetaceae include three small genera, the largest of which is *Rhizidiomyces* with five species. The thallus is monocentric, consisting of a single cell which bears a system of branched rhizoids sunken into the substratum, and which becomes converted into a sporangium. Sexual reproduction has not been observed. Resting spores are known only in the monotypic¹ genus *Latrostium*.

Rhizidiomyces apophysatus is parasitic on the oögonia of water molds of the family Saprolegniaceae and on the green alga *Vaucheria*. It has also been isolated from soil and pine pollen. Mycologists have found this fungus in Europe, North and South America, Asia, and Africa. It probably occurs all over the world.

Karling (1944) gives a full account of the life cycle in his studies of the fungus which he isolated from river water collected in the Amazon Valley of Brazil. The zoöspores (Figure 47A) swim for a time (25–90 minutes), before coming to rest on the host. They round up and soon germinate, producing a germ tube which penetrates the oögonial wall of the host and begins to branch (Figure 47B). At this time, a swelling is formed on the germ tube just inside the oögonial wall. As the rhizoidal system develops, the swelling enlarges and becomes an **apophysis** (Gr. *apo* = from + *physis* = growth) of the sporangium, which synchronously develops from the main part of the zoöspore on the surface of the host (Figure 47C). As the sporangium matures, it develops an exit papilla which elongates and forms the discharge tube (Figures 47D, E). Nuclear divisions have probably taken place in the meantime, and by this time the sporangial protoplast must be multinucleate. The protoplast now moves up and slowly emerges from the discharge tube as a naked protoplasmic mass (Figures 47F, G) which almost im-

¹ Containing only a single species.

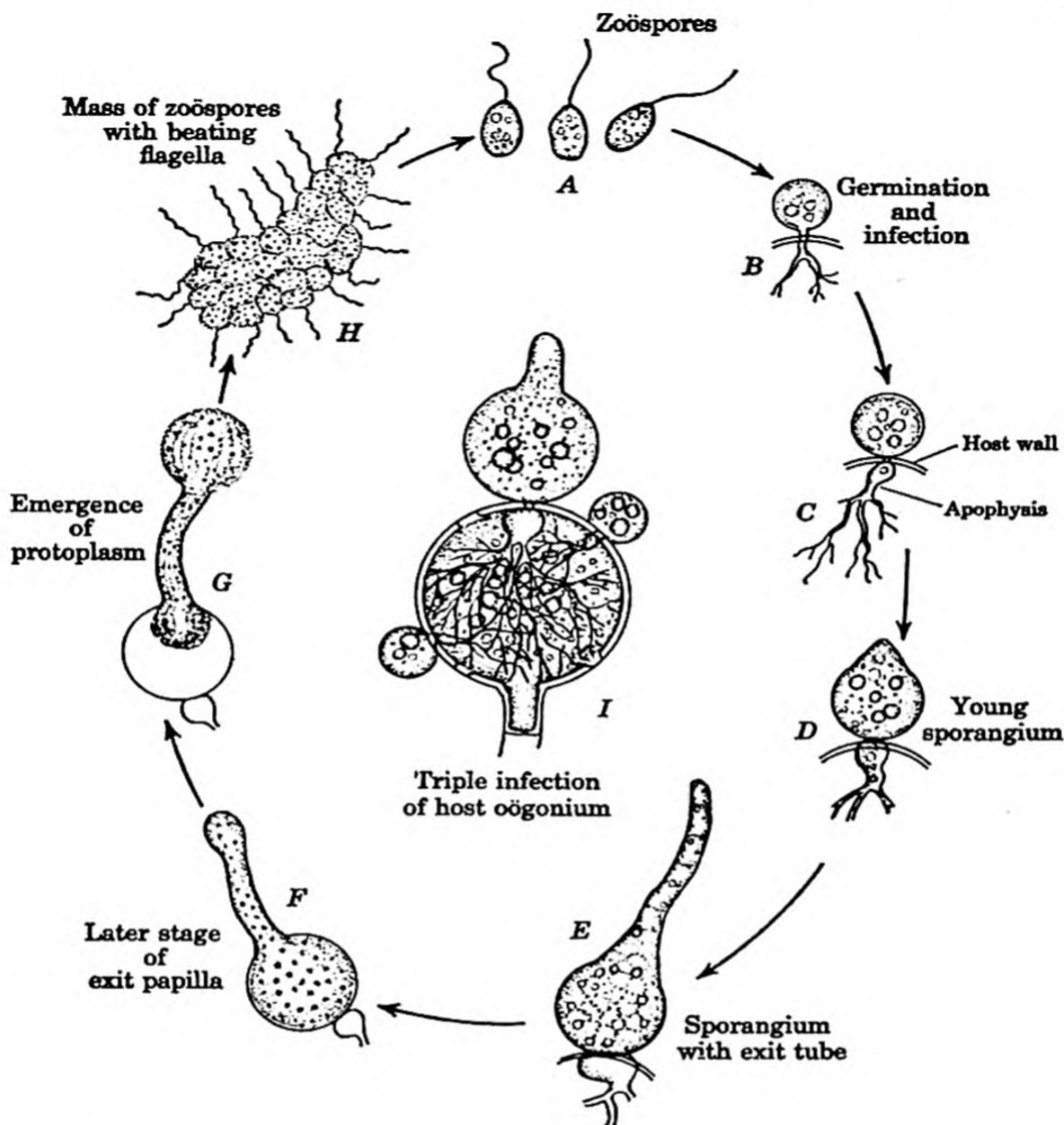


Figure 47. Life cycle of *Rhizidiomyces apophysatus*. Redrawn from Karling, 1944, *Am. Jr. Bot.*, 31:391-397.

mediately changes shape and becomes cleaved into zoospore initials through a process of furrowing. The zoospores soon become differentiated, the flagella are formed (Figure 47H), and the zoospores swim away. No sexual reproduction or resting spores are known.

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7 class OÖMYCETES water molds, white rusts, and downy mildews

Introduction. The class Oömycetes consists of fungi which reproduce asexually by means of biflagellate zoöspores, each bearing one tinsel flagellum directed forward and one whiplash flagellum directed backward. Zoöspores are borne in sporangia of various types.

The most advanced of the Oömycetes are terrestrial obligate parasites passing their entire life history in the host, and depending on the wind for the dissemination of their spores or spore-like sporangia. Even in these, however, the production of zoöspores continues to be common, a strong indication of their aquatic ancestral life.

The somatic structures of the fungi in this class range from a primitive unicellular thallus to a profusely branched, copious, filamentous mycelium, which grows abundantly in the substratum or in the surrounding medium. The majority of the Oömycetes are eucarpic. Both asexual and sexual reproductive structures occur in most species, but there are considerable gaps in our knowledge of many life histories in the group. In the highest forms, which are specialized parasites on plants, the tendency to produce several asexual generations during the growing season, but only one sexual generation, has become firmly established.

Zoöspores are produced throughout the class except in the most advanced species, in which the sporangium itself assumes the function of a spore and germinates directly by a germ tube which gives rise to the mycelium. Sexual reproduction is almost always heterogametangic. In the more primitive forms, the entire thallus acts as a gametangium. The formation of oöspores is characteristic of all but the most primitive species. Oöspores originate in the oögonia

and mature within them. The central part of the oögonium is differentiated into one or more oöspheres. These are typically uninucleate when mature. In some forms they are multinucleate, and the oösphere is then called a **compound oösphere**.

Classification. As considered here, the Oömycetes consist of four orders: Saprolegniales, Leptomitales, Lagenidiales, and Peronosporales. A simplified form of Sparrow's key to these orders is presented below.

KEY TO THE ORDERS OF THE CLASS OÖMYCETES

(Adapted from F. K. Sparrow, 1960)

- | | |
|--|-----------------------|
| A. Zoöspores always formed within the sporangium, diplanetic,* monoplanetic,* or, rarely, aplanetic | |
| B. Holocarpic or eucarpic; hyphae when present without constrictions | <i>Saprolegniales</i> |
| BB. Eucarpic; hyphae constricted | <i>Leptomitales</i> |
| AA. Zoöspores formed within the sporangium or, if not, then usually within an evanescent vesicle arising from the sporangium; monoplanetic, reniform | |
| C. Holocarpic | <i>Lagenidiales</i> |
| CC. Eucarpic | <i>Peronosporales</i> |

* For the definition of these terms see page 142 and Glossary.

Importance to Man. Of the four orders in this class, only the Peronosporales affect man's welfare to a great extent. A few species in the Saprolegniales attack economically important plants, and a few others cause serious diseases of fish, but taken as a whole they are of no great significance. The Peronosporales, on the other hand, include some of the most destructive parasites known, and at least two of them have had a hand—or should we say a hypha!—in shaping the economic history of an important portion of mankind. These are *Phytophthora infestans*, the cause of late blight of potatoes, and *Plasmopara viticola*, the cause of downy mildew of grapes.

order LAGENIDIALES

General Characteristics. Our modern concept of the Lagenidiales encompasses a rather small group of aquatic fungi parasitic on algae, water molds, small animals, and other forms of aquatic or semi-aquatic life. The somatic structure of these fungi is either a simple cell or a very short, unbranched or sparingly branched filament. Sexual reproduction takes place by gametangial copulation, with or

without a fertilization tube, and results in the formation of a thick-walled resting spore.

In unicellular species (*Olpidiopsis*)¹ the entire thallus acts as a gametangium. In filamentous species (*Lagenidium*) the filament first becomes divided into cells by the formation of septa, and then some or all of these cells change into gametangia or sporangia.

Sparrow (1960) divides the Lagenidiales into three families: the Olpidiopsidaceae, the Sirolpidiaceae, and the Lagenidiaceae. The Olpidiopsidaceae have a unicellular thallus. The two other families, especially the Lagenidiaceae, are more typical of the order. We shall, therefore, discuss only the Lagenidiaceae in this book to give you a general idea of the morphology and life cycle of these fungi.

family LAGENIDIACEAE

Life History. Although I can discuss with you a general life history for the Lagenidiaceae, the truth is that the life history of not a single species has been worked out completely. This remark implies no lack of appreciation for the splendid work of such men as Zopf, Scherffel, Cook, Couch, Dangeard, and Sparrow, who have studied these organisms; it merely indicates the difficulty of such an undertaking. These fungi are not easy to find, and most of them will not grow in culture under any known conditions. Furthermore, their nuclei are so minute that cytological studies are extremely difficult.

Here are some things we know about the Lagenidiaceae. The thallus of most is filamentous, but not well developed. There is no extensive mycelium to be found, only a small filament which may or may not be branched, growing in a cell of an alga or the body of some unfortunate microscopic animal that has been attacked. After the thallus reaches a certain stage of maturity, septa are formed which divide the tubular thallus into a few cells. Each of these cells now changes into a reproductive organ—a sporangium or gametangium.

The protoplast of a sporangium divides itself into a number of zoöspores, probably as many as there are nuclei in the sporangium, and the zoöspores escape through one or more exit tubes formed in the sporangial wall and penetrating through the host cell wall (if any) to the outside. In the genus *Lagenidium* a thin, bubble-like vesicle (*L. vesicula* = small bladder) develops at the mouth of the exit tube and makes the sporangium appear to be blowing a soap bubble (Figure 48C). The sporangial protoplast moves through the

¹ Gäumann (1952) places *Olpidiopsis* in the primitive class Archimycetes.

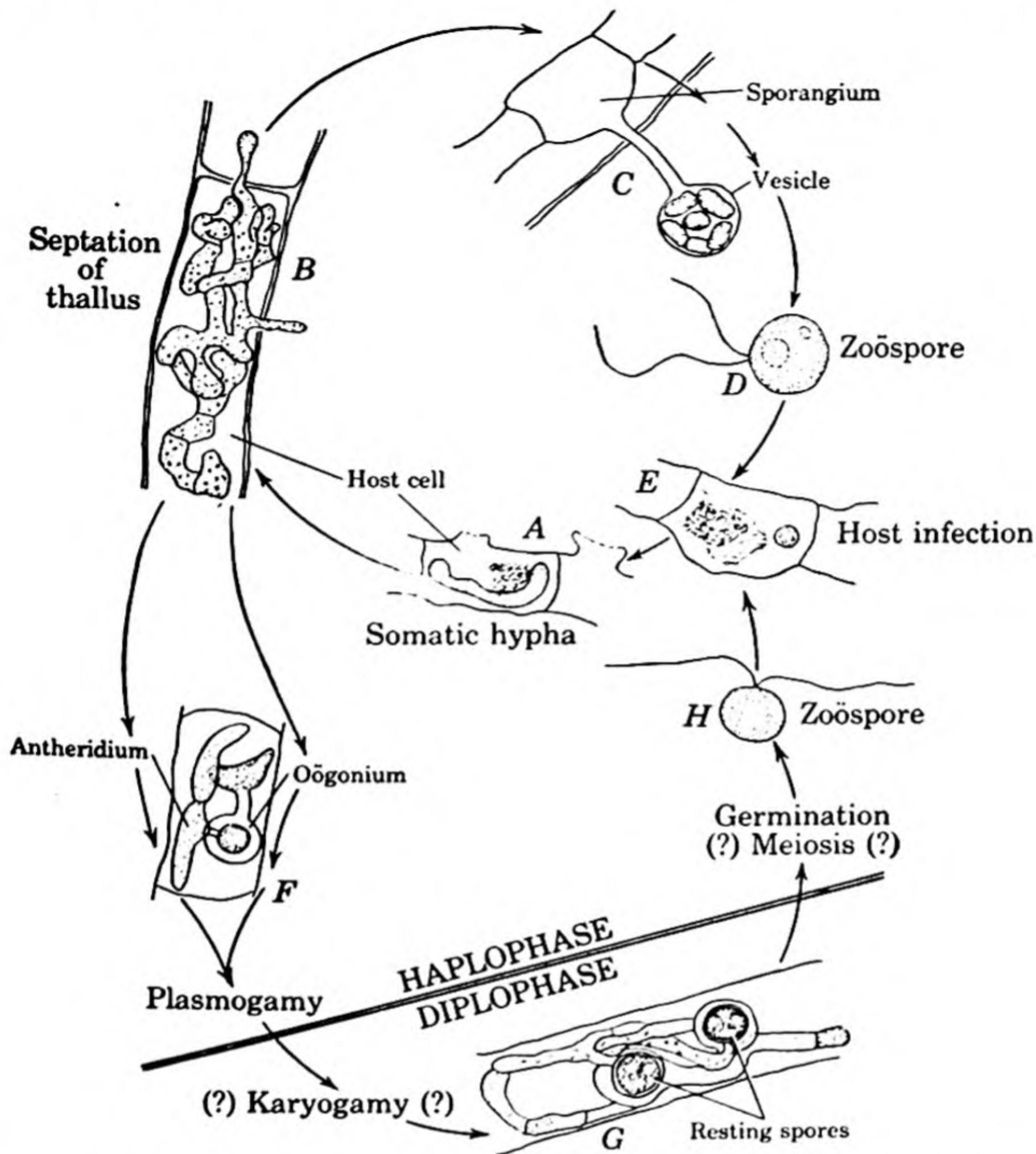


Figure 48. Life cycle of *Lagenidium rabenhorstii*. Redrawn from Cook, 1935, *Arch. Protistenk.*, 86:58-89.

exit tube into the vesicle, and the zoöspores become differentiated therein. They then become liberated into the surrounding water when the bubble bursts. The zoöspores swim around in the water for some time. Eventually they come to rest on a susceptible host and penetrate the wall or membrane. Inside the host the zoöspore gives rise to the thallus typical of the species.

Cook, Couch, Sparrow, and others have observed sexual reproduction in a number of species in the Lagenidiaceae. In all cases, they

have found that this takes place by the copulation of two gametangia and the passing of the protoplast of one gametangium into the other through a pore or a tube. The contacting gametangia, in some species, are formed from adjacent cells of the same thallus. In other species, gametangia from two thalli lying side by side come in contact. Dangeard (1903) found that the gametangia of *Myzocyttium vermicolum* are multinucleate, but that only one nucleus in each is actually functional; the others disintegrate. He observed that a thin wall is formed around the combined protoplasts and that karyogamy takes place soon after. The zygote is eventually transformed into a resting spore by the formation of a thick wall. These observations, made in 1903 by this French investigator, still remain unique in the cytology of the Lagenidiaceae.

Germination of the resting spore has been observed in only two species, according to Sparrow (1960). Meiosis presumably takes place—but has not been observed—when the oöspore germinates. In *Myzocyttium vermicolum* the “resting spore” releases zoöspores upon germination, *i.e.*, it acts as a zoösporangium.

Lagenidium rabenhorstii Zopf is one of the best-known species, although its cytology has not been worked out. Figure 48, constructed from the drawings which W. R. I. Cook published in 1935, will give you a clear idea of the life cycle of this species, which in many respects may be considered representative of the family.

order SAPROLEGNIALES

Introduction. The term water mold, though applicable to a number of other fungal groups as well, is customarily used to designate the Saprolegniales, for most of them occur abundantly in clear waters and are easily isolated. Many species are, however, soil-inhabiting.

The majority of species in this order are saprobic and are of little direct economic importance. A few of them, however, are important parasites. Some species of *Saprolegnia*, as *Saprolegnia parasitica*, cause diseases of fish and fish eggs, and may do significant damage to commercial or government fish hatcheries. The genus *Aphanomyces* contains several destructive parasites of the roots of vascular plants, causing serious diseases of sugar beets, peas, and other crops. *Aphanomyces euteiches*, which attacks a number of economically important hosts, is particularly prevalent.

Classification. The order Saprolegniales is divided into three families by Sparrow: the Ectrogellaceae, the Thraustochytriaceae, and the Saprolegniaceae. The Ectrogellaceae include one-celled, holo-

carpic organisms parasitic on algae. The Thraustochytriaceae, consisting of four species parasitic on marine algae, have a rhizoidal system which anchors the minute thallus to the host. No mycelium is developed by any species in either of these families. The Saprolegniaceae are considerably more advanced than either of the other two families and contain a much larger number of species. They may be regarded as typical of the order and are the only ones to be discussed here.

family SAPROLEGNIACEAE

Occurrence, Isolation, and Laboratory Cultivation. The Saprolegniaceae are among the most ubiquitous of aquatic fungi. They are present in most bodies of fresh water. Some species, able to withstand a certain degree of salinity, live in brackish waters of estuaries as well, when salinity does not exceed 2.8 per cent. Higher salinities limit the distribution of these fungi (TeStrake, 1959). Saprolegniaceae are also abundant in moist soils. Although they have not been reported from all parts of the world, there is little doubt that they are universally distributed and that we need only look for them in order to find them.

In addition to being widely distributed, the Saprolegniaceae are among the easiest fungi to isolate and cultivate in the laboratory. To isolate the Saprolegniaceae, go to the nearest pond and fill a quart jar half full of water. Add some bait in the form of three or four dead flies, split boiled hemp seeds, split boiled wheat, or corn grains. In a few days you should have good colonies which may then be transferred to sterile culture dishes, each containing 25 ml. of half and half autoclaved tap water and sterile distilled water. If no ponds are near by, some soil collected 1 or 2 inches below the surface and poured into a quart jar half full of autoclaved water should give good results when properly baited. Pure cultures are more difficult to obtain and require special techniques.

Somatic Structures. The Saprolegniaceae are characterized by a profusely branched, coenocytic mycelium easily visible as it forms a colony around some bit of decaying plant or animal tissue in water. The hyphal walls contain cellulose. Septa are formed in the mycelium just below the reproductive organs, separating them from the somatic hyphae, which generally remain aseptate. The hyphae vary considerably in diameter. In some species they are very wide; in others they are characteristically fine.

The nutritive requirements for growth of some of the Saprolegniaceae have been investigated, and a general picture is beginning to appear (Klebs, 1899; Volkonsky, 1933; Bhargava, 1943–1946; Whiffen, 1945; Reischer, 1951; Dayal, 1960; Papavizas and Davey, 1960a). Glucose seems to be the best source of carbon for most species; maltose, starch, and glycogen are available to several; fructose, mannose, sucrose, and ethanol are utilized by some. In general the Saprolegniaceae appear unable to utilize nitrates, but grow well on media containing organic N in the form of peptone or any one of a number of amino acids. Whether ammonium salts can serve as the sole source of N is controversial, but the evidence seems to indicate this is true for certain species and under some conditions. Most species investigated are able to synthesize all the vitamins required for growth. Inorganic growth requirements include Mg, Ca, Zn, Mn, Fe, and S. Sulphates apparently cannot be utilized, but S may be conveniently supplied in organic form as cysteine, cystine, glutathione, or methionine. A pH range from 4.0 to 6.0 has been found to be optimal for the growth of five species.

Asexual Reproduction. Long, cylindrical, terminal zoösporangia are typically produced by members of this family. In general the sporangia are somewhat greater in diameter than the hyphae on which they are produced. The young sporangia are full of dense, granular protoplasm which gives them a somewhat brownish appearance by transmitted light under the microscope. Sporangia are usually terminal (Figure 49A).

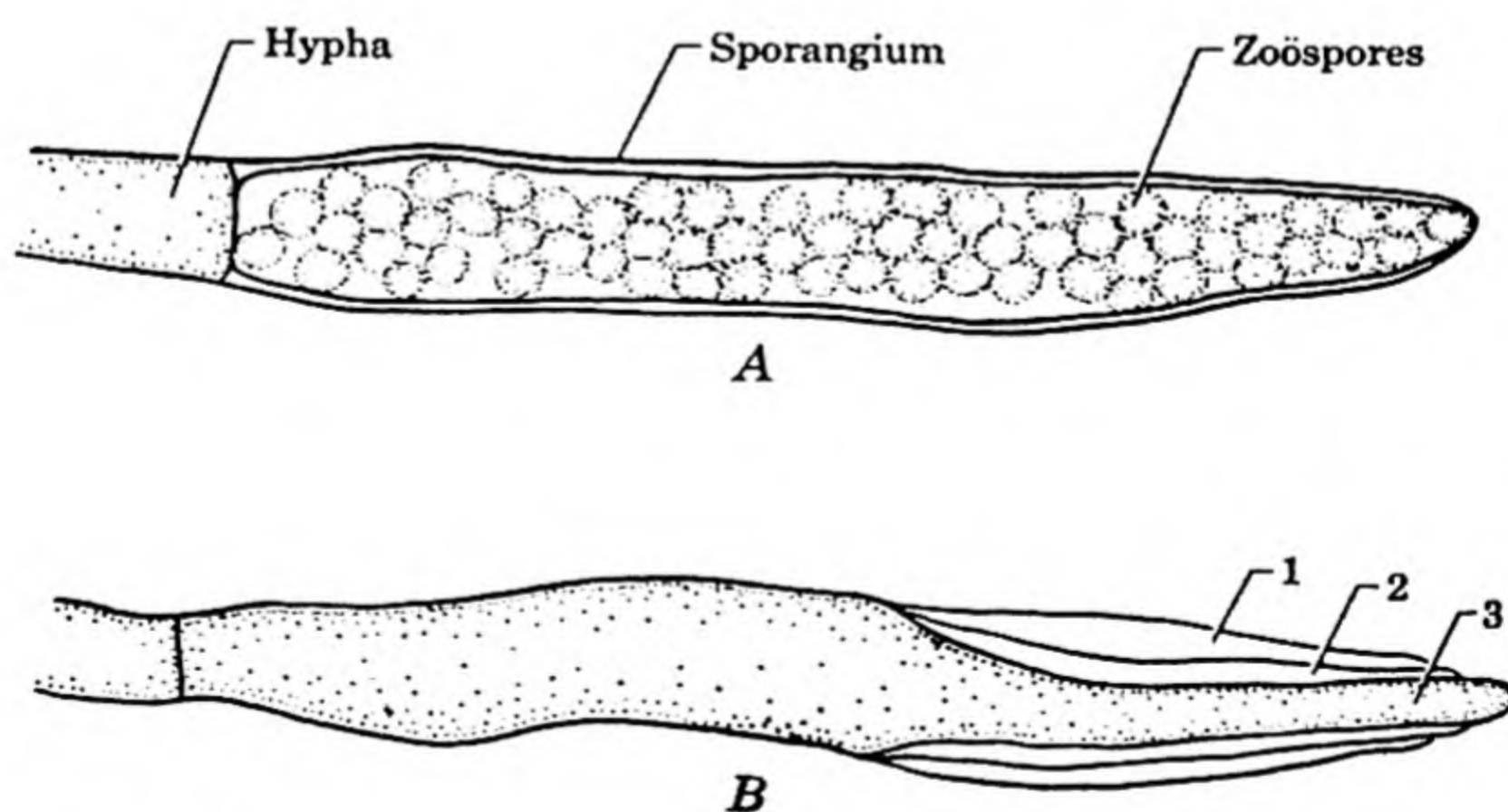


Figure 49. A. Mature sporangium of *Saprolegnia* sp. B. Internal proliferation. 1, 2. Empty sporangial cases. 3. Developing sporangium.

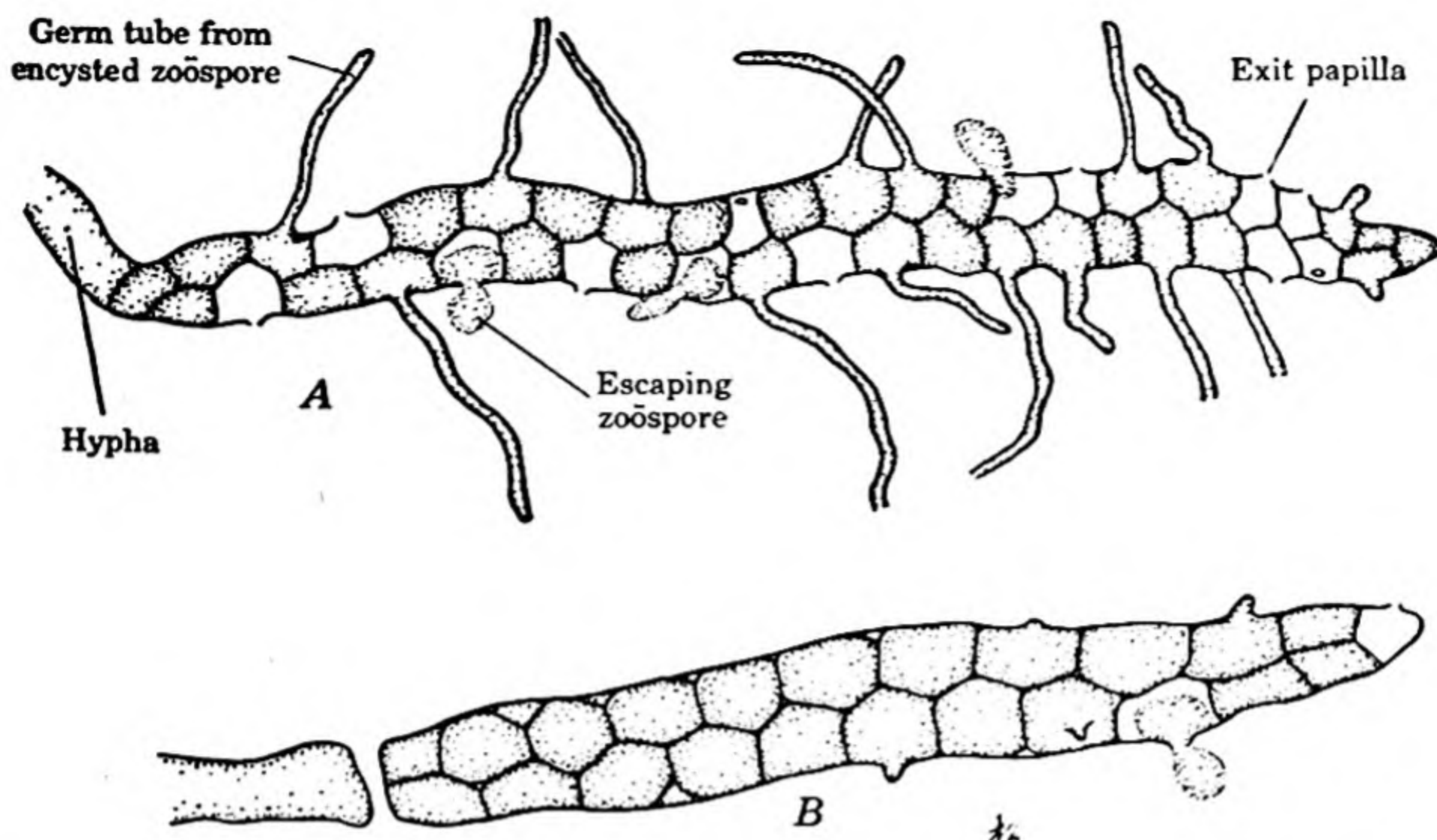


Figure 50. *Dictyuchus* sp. A. Sporangium attached to hypha. Some zoospores have escaped through individual exit papillae, leaving empty cells; two are in the process of escaping; several have encysted within the sporangium and have produced germ tubes. B. Detached sporangium.

The exact conditions which induce the mycelium of the Saprolegniaceae to sporulate have not been studied in detail, little knowledge having been added since the classic experiments of Klebs (1898–1900). Klebs found that he could maintain *Saprolegnia* cultures in the assimilative stage for 2½ years if he provided them with fresh supplies of nutrients. To induce sporangial formation the cultures were transferred to water.

Sporangial proliferation is an interesting phenomenon in the Saprolegniaceae. It may occur in various ways. In the genus *Saprolegnia* it takes place as follows. When a sporangium has emptied its contents of spores, another or secondary sporangium often is initiated at the basal septum, and grows through the first sporangium, maturing within it or beyond it. Several sporangia may thus be formed one within the other, each maturing and shedding its spores before the next one is formed (Figure 49B). As a general rule, the sporangia of the Saprolegniaceae remain attached to the somatic hyphae throughout their lives, and even after they have discharged their spores. The genus *Dictyuchus* is an exception, the sporangia commonly falling off the hyphae at maturity (Figure 50).

Zoöspores and Zoöspore Behavior. Two types of zoöspores occur in the Saprolegniaceae. The primary zoöspores are pear-shaped and bear their two flagella at the apex; the secondary zoöspores are kidney-shaped and bear two oppositely directed flagella at the concave side of the zoöspore.

Species which produce only one type of zoöspore are **monomorphic** (Gr. *monos* = alone, one + *morphe* = shape, form). Species which produce both types of zoöspores are **dimorphic** (Gr. *dis* = twice + *morphe* = shape, form).

The behavior of the zoöspores differs in different genera and is an important taxonomic character. The several types of zoöspore behavior may be illustrated by the following examples.

In the genus *Pythiopsis*, the zoöspores released from the zoösporangium are primary zoöspores. They swarm for some time, then come to rest, become rounded, encyst, and eventually germinate, each putting forth a germ tube which grows into a hypha. There is thus typically only one swarming period and only one type of zoöspore produced. Such behavior is called **monoplanetism**, and the species behaving thus are called **monoplanetic** (Gr. *monos* = alone, only + *planetes* = wanderer).

The genera *Saprolegnia*, *Isoachlya*, *Leptolegnia*, and *Leptolegniella* produce both types of zoöspores in succession. The primary zoöspores are released from the sporangium, and after a period of swarming encyst. Instead of germinating by germ tube, however, each cyst gives rise to a secondary zoöspore which embarks upon a second swarming period. Encystment and germination by germ tube follow. Species in which two swarming periods occur, involving two types of zoöspores, we call **diphanetic**, and the phenomenon **diphanetism** (Gr. *dis* = twice + *planetes* = wanderer). In *Saprolegnia*, both swarming periods are of considerable duration. In *Achlya*, the primary zoöspores encyst just outside the mouth of the sporangium as soon as they are released. Eventually they germinate and release secondary zoöspores. *Achlya* thus exhibits a strong tendency to suppress the first swarming period.

In the genus *Dictyuchus* no primary zoöspores are liberated. Instead, they encyst within the sporangium and each releases a secondary zoöspore which escapes from the sporangium, swarms for a time, and encysts. After a resting period each of these cysts releases another secondary zoöspore which in turn swarms and encysts. This process may be repeated several times, all swarming zoöspores being of the secondary type. Such a phenomenon is called **repeated**

zoöspore emergence, or polyplanetism (Gr. *poly* = much + *planetes* = wanderer).

In the genus *Thraustotheca*, the primary zoöspores encyst within the sporangium and eventually liberate secondary zoöspores which swarm but once.

In *Geolegnia*, which possibly represents the culmination of this evolutionary series, both swarm periods have been suppressed and no zoöspores are formed. Each of the aplanospores which escape from the sporangium germinates by a germ tube. *Geolegnia* is thus **aplanetic** (Gr. *a* = not + *planetes* = wanderer). It is thought that an ancestral type resembling *Geolegnia* may have given rise to the fungi of the class Zygomycetes, which we shall discuss in Chapter 9.

It is important to remember at this point that organisms do not behave in the same way under all conditions. Thus, an organism which is usually monoplanetic or usually diplanetic may at times exhibit polyplanetism, as has been shown with *Pythiopsis* and *Achlya*, respectively. What causes this behavior is not known.

Chlamydospores. Another method of asexual reproduction in the Saprolegniaceae, in addition to the production of sporangia and sporangiospores, is by means of chlamydospores (Figure 51), sometimes called **gemmae** (sing. *gemma*; L. *gemma* = bud). These are

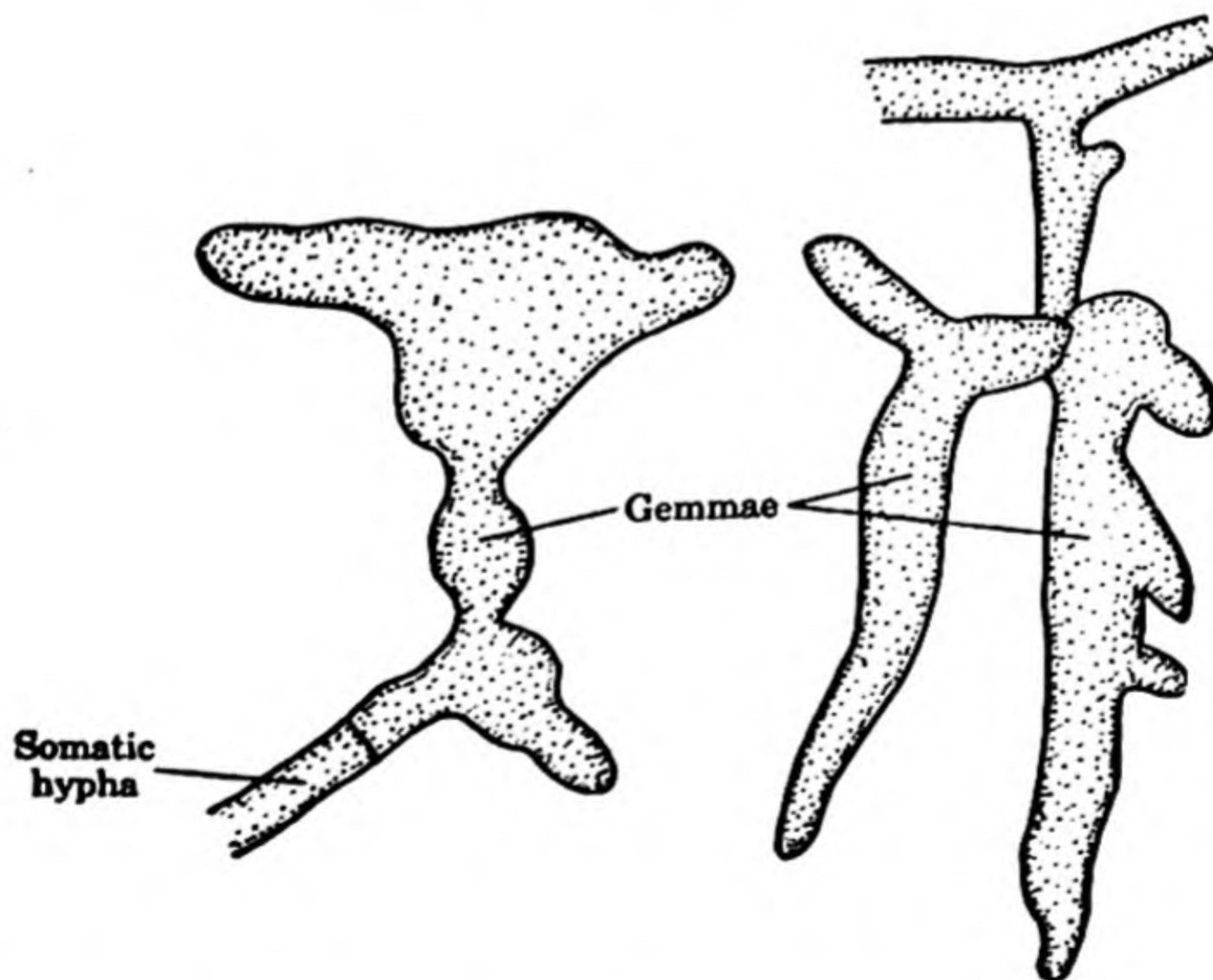


Figure 51. Gemmae of *Saprolegnia*. Redrawn from Coker, 1923, *The Saprolegniaceae*, by permission of University of North Carolina Press, Chapel Hill.

generally borne terminally, either singly or in chains. In the latter event, they become separated after maturing. Gemmae germinate by means of germ tubes which either grow into hyphae or develop into short-stalked sporangia typical of the species.

Sexual Reproduction. Sexual reproduction in the Saprolegniaceae is by means of gametangial contact, the passage of the male gametes into the female gametangium taking place through a fertilization tube. The sex organs are generally terminal, but intercalary oögonia also may be formed (Figure 52). The oögonium is usually globose, its entire contents differentiating into one or more globular, finally uninucleate oöspheres. The elongated and multinucleate antheridia originate either on the same hyphal branch on which the oögonium is attached, on a different branch, or on an entirely different thallus. One or more antheridia become attached to the oögonium, pierce it, and branch out, sending one branch to each oösphere within the oögonium. One nucleus of the antheridium now passes through each fertilization tube into each oösphere and fuses with the egg nucleus therein. Fertilized oöspheres develop thick walls and are converted into oöspores. In the mature oöspores of the Saprolegniaceae the fatty reserve is stored in the form of oil droplets characteristically arranged in different species. These arrangements are of considerable taxonomic value. After a period of rest, the oöspore germinates by means of a hyphal tube which shortly afterwards gives rise to a zoösporangium typical of the species. Although karyogamy has been demonstrated in a considerable number of species, in others the oöspores develop parthenogenetically. In some species, no antheridia are known to be formed.

The majority of the Saprolegniaceae are hermaphroditic and homothallic, producing compatible antheridia and oögonia on the same thallus. However, some dioecious species are also known, which require two individuals for sexual reproduction, one male, one female. *Achlya bisexualis* and *Achlya ambisexualis*, which are dioecious, were used by Dr. John R. Raper (1939–1951) in his now classic investigations on the sexual mechanism involved.

Raper demonstrated conclusively that, when potentially male and female thalli grow in close proximity, a system involving at least four distinct hormones becomes operative and initiates the sexual process. Hormone A (actually consisting of several entities) is liberated by the somatic hyphae of the female thallus and induces the formation of antheridia by the hyphae of the male thallus. The antheridial branches now produce hormone B, which induces the

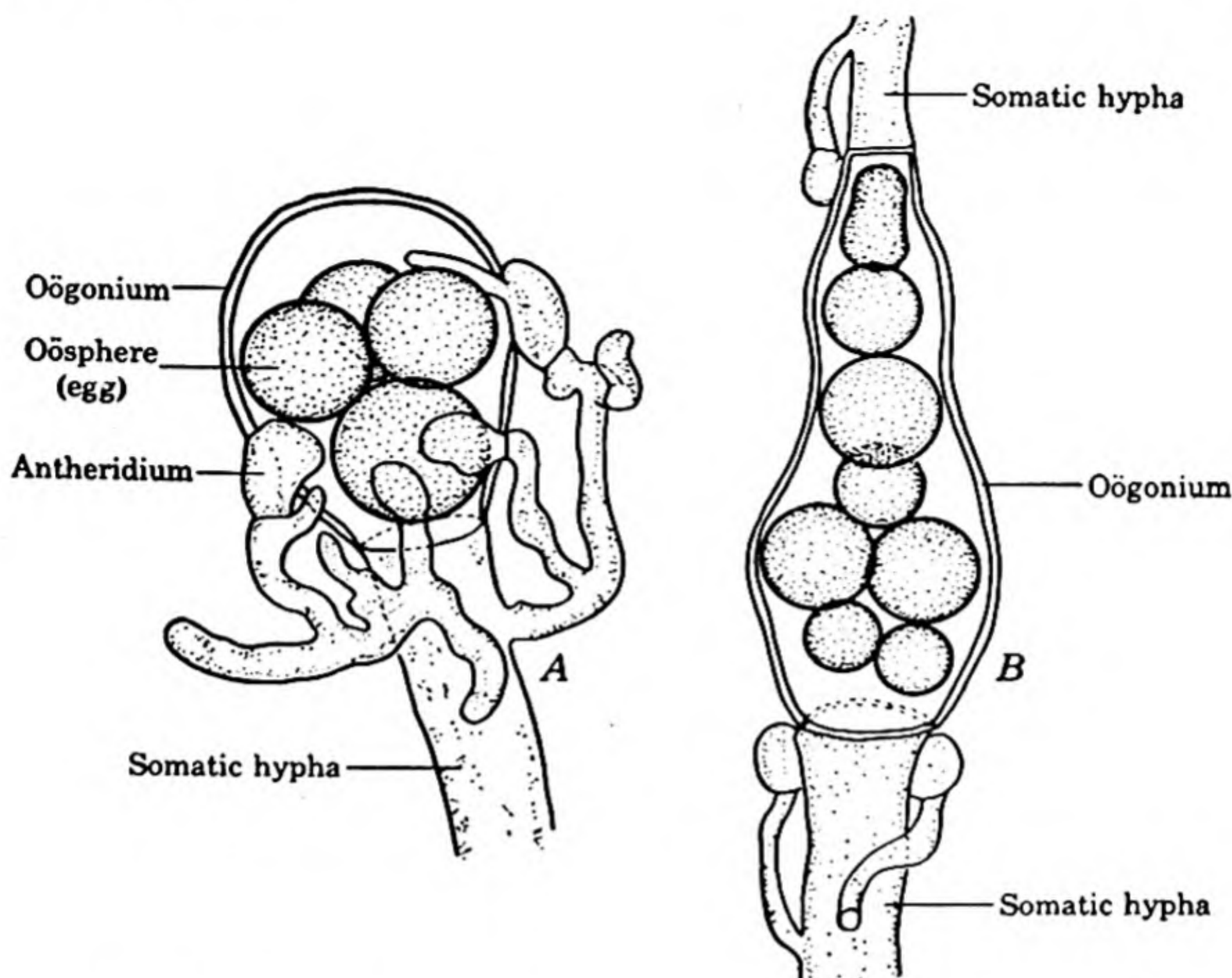


Figure 52. *Saprolegnia littoralis*. A. Terminal oögonium with antheridia. B. Intercalary oögonium. Redrawn from Coker, 1923, *The Saprolegniaceae*, by permission of University of North Carolina Press, Chapel Hill.

formation of oögonial initials by the female thallus. These oögonial initials produce hormone C, which attracts the antheridial branches of the male thallus to the oögonial initials of the female thallus. Upon contact, the delimitation of antheridia is induced. The antheridia finally produce hormone D, which induces the formation of a wall at the base of each oögonium, thus delimiting the female sex organs. These processes are illustrated in Figure 53.

Life History. Several genera of water molds belong to the Saprolegniaceae. The most common are *Saprolegnia*, *Achlya*, and *Dictyuchus*. The genus *Saprolegnia* will be taken as an example of the general life history of members of this family (Figure 54).

The somatic portion of the thallus is composed of two types of hyphae: first, the rhizoidal hyphae, which enter the substratum, be it the body of a dead fly or a dead seed of some flowering plant, and which serve to anchor the organism and to absorb nourishment; sec-

ond, the mass of profusely branched hyphae (Figure 54A) on the outside of the substratum, which forms the visible colony of the organism and on which the reproductive organs are formed.

Under the proper environmental conditions, the hyphae give rise to sporangia (Figure 54B). Typically, the sporangia are elongated,

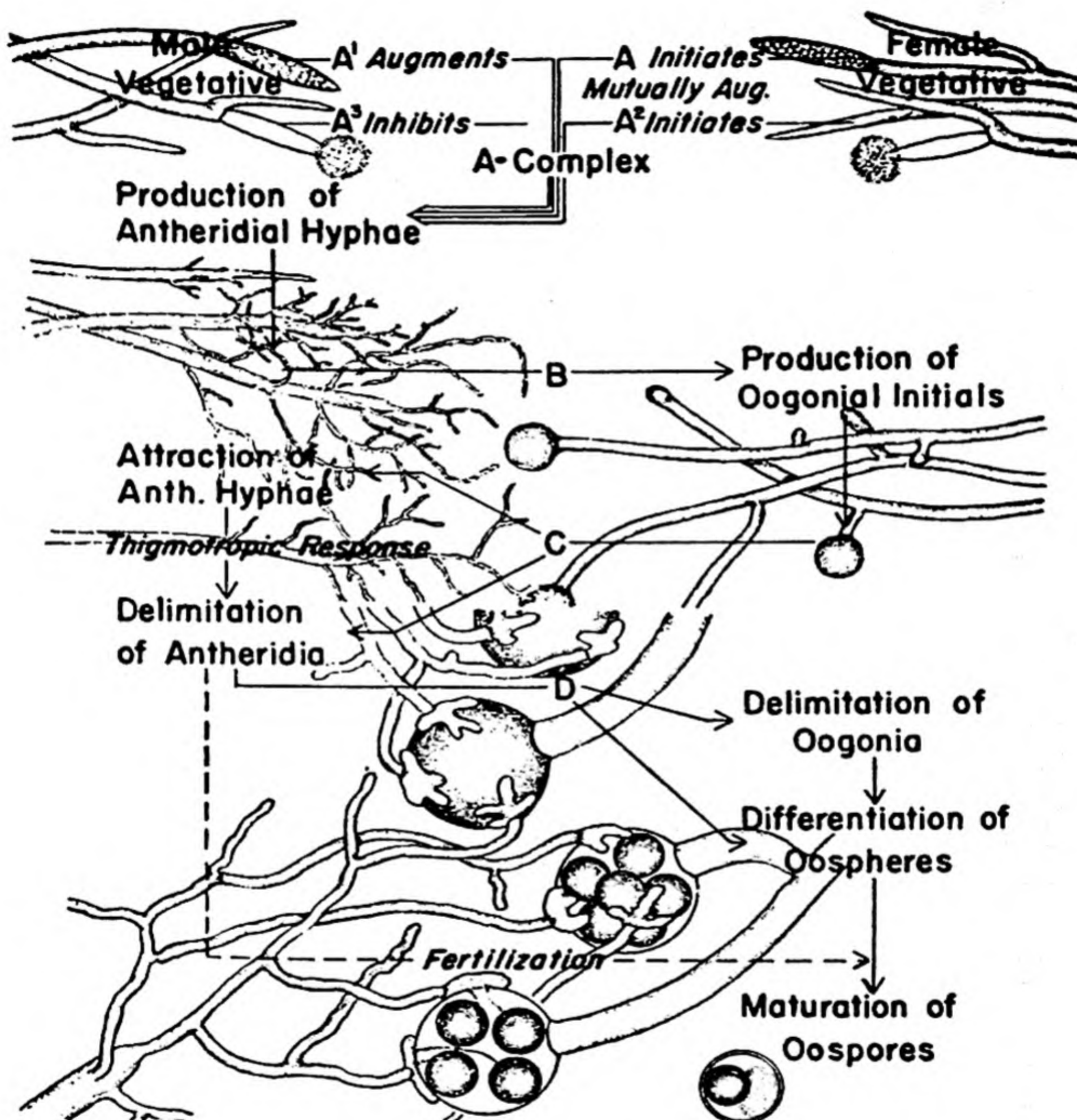


Figure 53. A semidiagrammatic representation of the sexual progression in heterothallic species of *Achlya* relating the sequence of morphological developments to the origins and specific activities of the several sexual hormones. Reproduced from Raper, by permission, from *Specificity and growth*, 1955, Princeton University Press, Princeton, N. J.

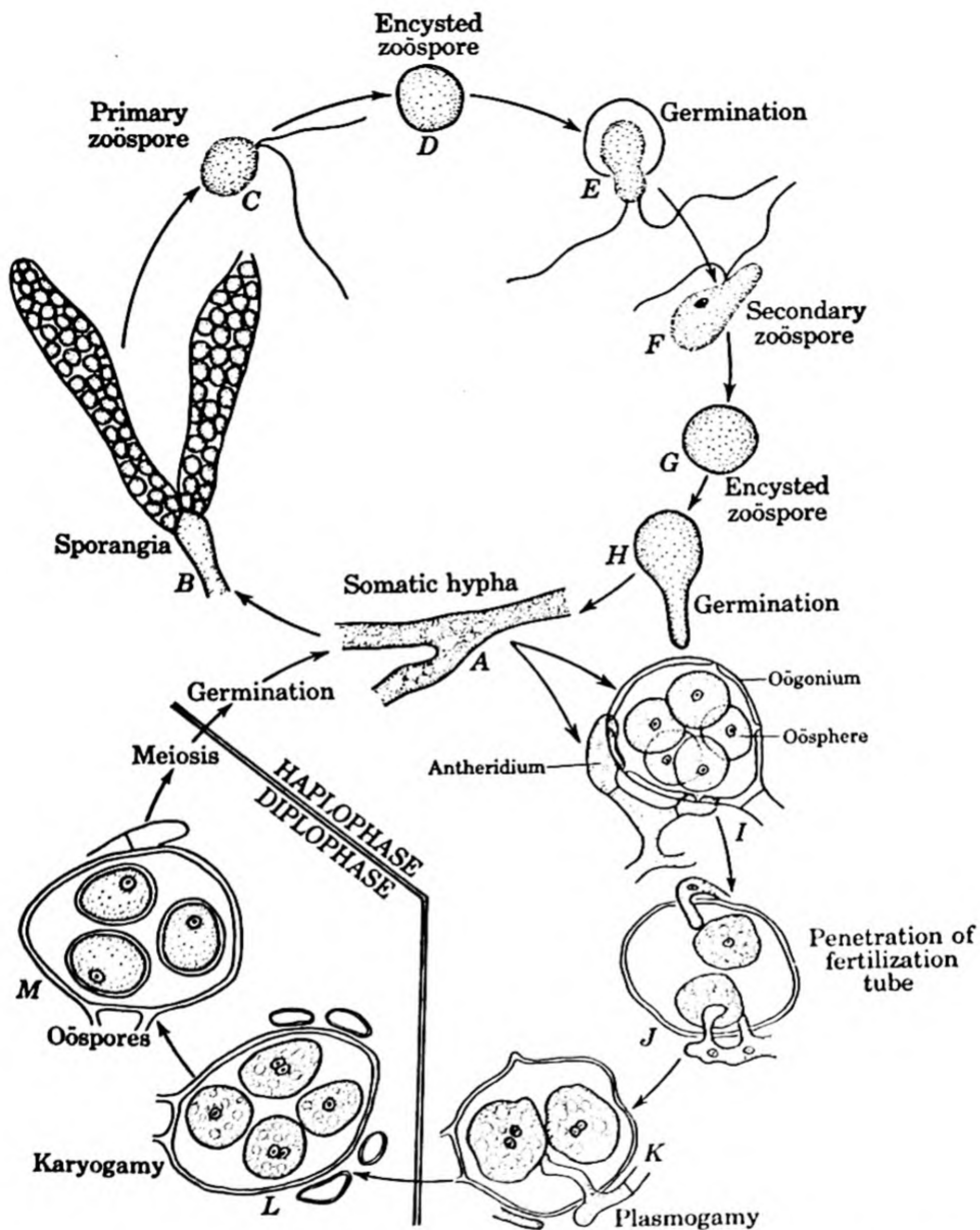


Figure 54. Life cycle of *Saprolegnia* sp. C, E, F, constructed; J–L, redrawn by permission from *Cryptogamic botany*, Vol. I, by G. M. Smith, 1938, McGraw-Hill Book Co., New York.

tapering structures borne at the tips of somatic hyphae, and separated from them by a septum. The sporangia are densely filled with protoplasm in contrast to the somatic hyphae, which are only lined with a thin protoplasmic layer. As the sporangium develops, and before the basal septum is formed, a large number of nuclei stream into the sporangium from the somatic hypha below. The sporangial protoplast is now divided into as many portions as there are nuclei, and each portion develops into a spore, the whole protoplast being utilized for spore formation.

The method of escape of the zoöspores varies with different genera. In *Saprolegnia*, an opening develops at the tip of the sporangium, and the primary zoöspores escape into the surrounding water. Here they swim about for some time, come to rest, and encyst. After a short resting period, a thin papilla develops on the cyst, its tip dissolves, and a reniform zoöspore with two lateral flagella creeps out. After a short swarming period, encystment follows. The encysted spore now germinates by a germ tube which develops into a hypha and initiates a new colony. Diplanetism is the rule in *Saprolegnia* (Figures 54C-H). By proliferation or branching, sporangia continue to be formed, several asexual generations following one another.

When conditions favorable to sexual reproduction appear, the somatic hyphae give rise to oögonia and antheridia (Figure 54I). Oögonia range from globose to oblong in shape, the globose type predominating. They have relatively thick walls as compared with the walls of somatic hyphae, and each when mature contains from one to many free oöospheres, most species producing several. A single nucleus is present in each mature oöosphere.

The antheridia are much smaller than the oögonia. They are multinucleate, elongated bodies borne terminally on slender branches of the somatic hyphae. They are often borne on the same hypha which bears the oögonium, and arise immediately below it, but in some species they are formed on different hyphae.

The antheridia, when fully formed, become attached to the oögonia, one or more for each oögonium. Fertilization tubes originating in the antheridium penetrate the oögonial wall and reach the oöospheres (Figure 54J). Upon entering the oögonium, a fertilization tube may branch out and send one branch to each oöosphere. Even when more than one antheridium contacts the oögonium, an oöosphere is, as a rule, approached by only one fertilization tube. The antheridial nuclei now migrate from the antheridium to the oöospheres through the fertilization tubes; one nucleus enters each oöosphere, approaches its nucleus, fuses with it, and forms a diploid zygote nucleus (Figures

54K, L). After fertilization, a thick wall develops around each oösphere, converting it into an oöspore. The wall of the oöspore is smooth (Figure 54M). After a prolonged rest period, the oöspores are liberated from the disintegrated oögonial wall and germinate, each oöspore producing a germ tube. Shortly thereafter, a sporangium generally develops at the tip of this hypha, completing the life cycle. Meiosis occurs during the germination of the oöspore (Ziegler, 1948, 1953).

order LEPTOMITALES

The Leptomitales constitute a small order of about twenty species of saprobic, aquatic Phycomycetes. In general they resemble the Saprolegniales, under which they were included as the family Leptomitaceae until 1927, at which time, as a result of her extensive studies, Dr. Bessie B. Kanouse of the University of Michigan established the order Leptomitales.

The somatic hyphae of the Leptomitales, though truly aseptate, are nevertheless constricted at intervals, and the constrictions are sometimes plugged with granules of cellulose, giving the appearance of septa. This is the outstanding morphological characteristic of the order which distinguishes it from the Saprolegniales (Figure 55A).

Some interesting differences in S and N nutrition between the Saprolegniaceae and the Leptomitales have also been discovered. Whereas the Saprolegniaceae, you will remember, appear unable to utilize sulfates, the Leptomitales reduce sulfates and utilize the S in their metabolism. Members of both groups appear unable to utilize nitrate N, but some Saprolegniaceae can probably use ammonium N, whereas the Leptomitaceae seem unable to do so.¹

Asexual reproduction takes place by means of terminal zoösporangia from which biflagellate zoöspores are released. The species may be diplanetic or monoplanetic. The sporangia of some species are elongated and of the same diameter as the somatic hyphae. Many species, however, produce pyriform sporangia (Figure 55B). This is an important detail, for, as we shall see presently, the oval or round shape represents an advanced development in the evolution of the sporangium, and the presence of pyriform sporangia in this order, together with other factors, may be an indication that the Leptomitales are intermediate between the Saprolegniales and the Perono-

¹ But see Gilpin (1954) for some contradictory conclusions on N requirements of *Apodachlya*.

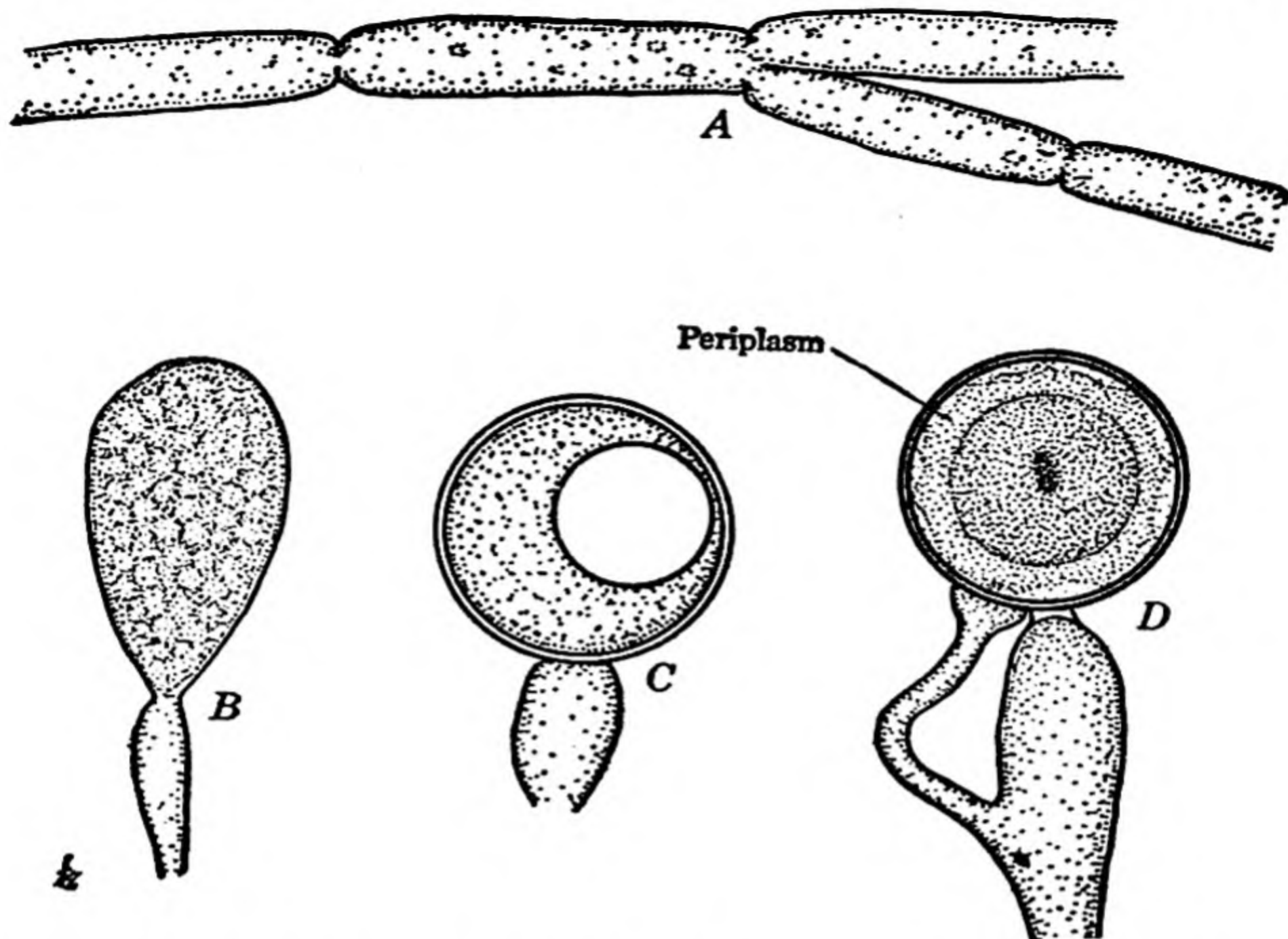


Figure 55. Leptomitales. A–C. *Apodachlya pyrifer*. A. Somatic hypha showing constrictions. B. Sporangium. C. Oöspore. D. *Rhipidium americanum*. Periplasm depositing wall of oöspore. D, redrawn from Thaxter, 1896, *Bot. Gaz.*, 21:317–331, by permission of University of Chicago Press, Chicago.

sporales. Although oval sporangia are not unknown in the Saprolegniales, their sporangia are typically elongated. The opposite is true of the Peronosporales.

Sexual reproduction takes place as in the Saprolegniales, by gametangial contact. In most Leptomitales, however, each oögonium contains but a single oösphere (Figure 55C). In most species the oösphere does not lie free within the oögonium, but is surrounded by a rather thick layer of protoplasm, the **periplasm** (Gr. *peri* = around + *plasma* = a molded structure) (Figure 55D). This is the first time we have encountered periplasm in the Oömycetes.¹ We shall see that it becomes well established in the Peronosporales.

Two families, the Leptomitaceae and the Rhipidiaceae, with seven genera are now recognized. For further details consult Sparrow (1960).

¹ In the small genus *Pythiella* of the Ectrogellaceae (Saprolegniales) distinct periplasm is present in the oöspores (Couch, 1935).

order PERONOSPORALES

The Peronosporales represent the highest development of the class Oömycetes. This large order of fungi includes aquatic, amphibious, and terrestrial species, culminating in a group of highly specialized obligate parasites. Many species in this order are destructive parasites of economic plants, frequently causing epiphytotics with tremendous losses to crops. The damping-off fungi, the white rusts, and the downy mildews all belong to this order, which includes several hundred species.

Somatic Structures. The mycelium of the Peronosporales is well developed, consisting of coenocytic, stout hyphae which branch freely. A large number of species in this order produce haustoria by means of which the hyphae obtain nourishment from the host cells. The haustoria may be knob-like, elongated, or branched within the host cells (Figure 56). The hyphae of the parasitic species are intercellular or intracellular, those of the most specialized parasites growing between the cells.

Asexual Reproduction. Asexual reproduction is in principle the same as in the Saprolegniaceae and the Leptomitales, but differs in detail. Thus, although a sporangium is formed which typically produces zoöspores, the typical sporangium is strikingly different from that in the previous orders, being oval or lemon-shaped in most species, rather than elongated. Although in the lower Peronosporales the sporangia are borne on ordinary somatic hyphae and remain attached even after the zoöspores have been released as in the Saprolegniaceae, in the more advanced types the sporangia are borne on sporangiophores and are deciduous upon maturity, depending on the wind for dissemination. In this respect, the whole sporangium acts as a spore, and in the highest forms actually germinates by a germ tube instead of producing zoöspores. The majority of species, however, produce zoöspores, which are reniform, biflagellate, and monoplanetic. Diplanetism and polyplanetism occur in a very few species. Upon their release from the sporangium, the zoöspores swarm for some time, come to rest, encyst, and germinate each by a germ tube which develops into the mycelium.

Sexual Reproduction. Sexual reproduction in the Peronosporales is by means of well-differentiated oögonia and antheridia borne on the same or on different hyphae. The oögonium, which is generally globose, contains, with few exceptions, but a single uninucleate or multinucleate oösphere, surrounded by a layer of periplasm. The antherid-

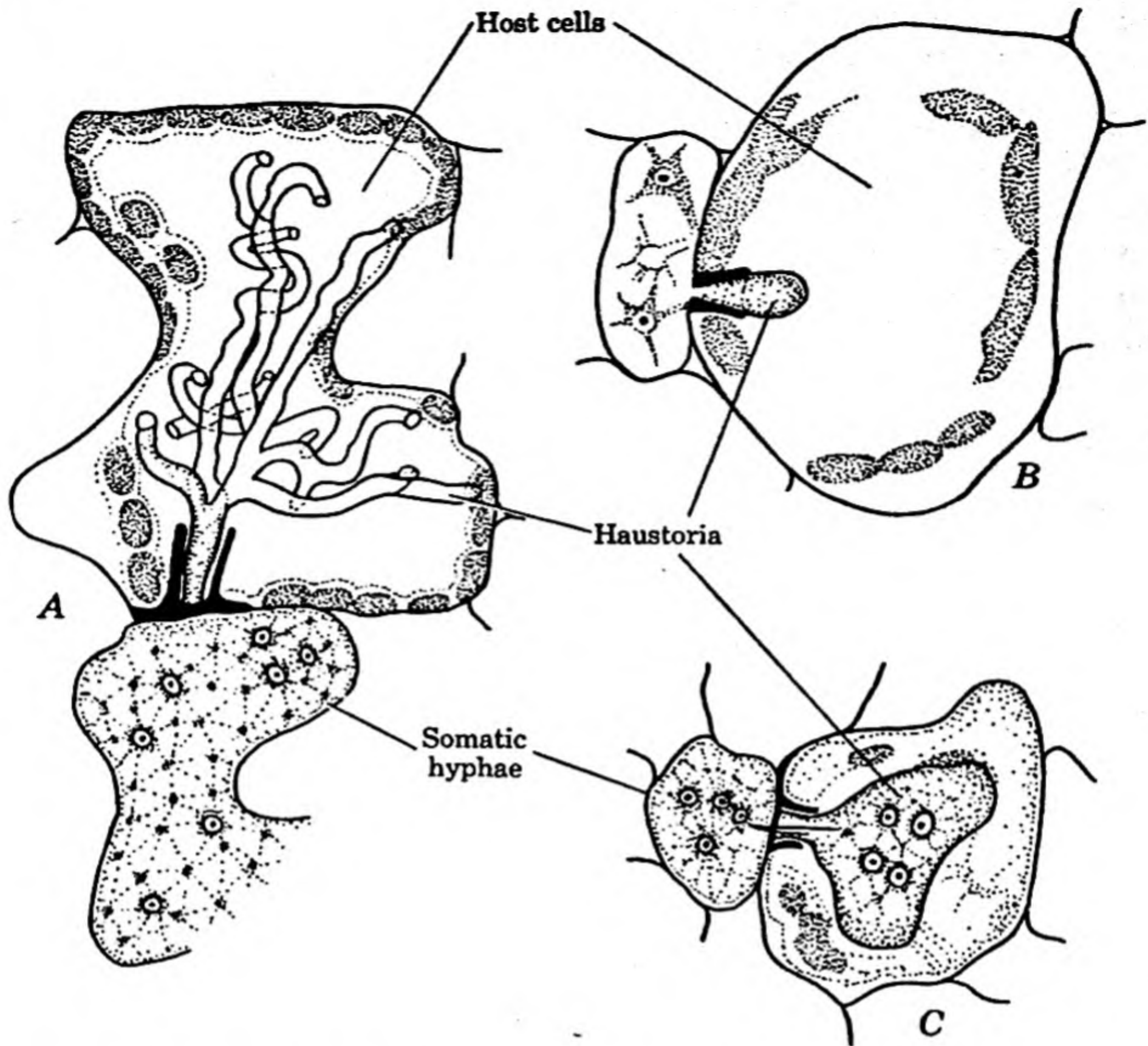


Figure 56. Haustoria of the Peronosporaceae. *A. Peronospora ficariae.* *B. Plasmopara pygmaea.* *C. Peronospora parasitica.* Redrawn from Clum, 1950, M.S. Thesis, University of Wisconsin.

ium is uninucleate or multinucleate, depending on the species. When gametangial contact is effected, a fertilization tube is formed by the antheridium, pushes through the oögonial wall and the periplasm, and reaches the oösphere. The male nucleus or nuclei then pass through the fertilization tube and are shed into the oösphere. If the latter is uninucleate, a single male nucleus fuses with the female nucleus and forms the zygote. If the oösphere is multinucleate, one or more of its nuclei may be functional, the number of male nuclei that will effect fertilization being regulated accordingly. Thus, either a single zygote nucleus or a number of diploid nuclei may result from a simple or multiple fertilization, respectively.

After fertilization, the oösphere develops a thick wall and changes

into an oöspore. The periplasm probably serves as nourishment for the developing oöspore. It is also responsible for the external thickenings and ornamentations which it deposits on the oöspore walls of some species. The oöspore wall is a triple wall consisting of an outer, a middle, and an inner layer. The outer wall may be smooth or variously sculptured or ornamented; it may be spiny, warty, wavy, ridged, or otherwise marked. The mature oöspore generally lies free within the oögonial wall, but in many species adheres to the latter so closely that it appears to be united with it. Only in the genus *Sclerospora* is the oögonial wall actually fused with the oöspore wall. After overwintering, the oöspores germinate in the spring, either by giving rise to zoöspores, thus behaving as zoösporangia, or by putting out germ tubes which soon afterwards produce sporangia. The type of germination varies with the species.

Classification. The classification of the Peronosporales is based mostly on the characters of the sporangia and the sporangiophores. The latter are strikingly characteristic of many groups, and the variation among them lends itself to taxonomic treatment. This is in contrast to the sexual (oöspore) stage in which the variations are not so obvious.

We divide the order Peronosporales into three families on the basis of sporangiophore characters: the Pythiaceae, the Albuginaceae, and the Peronosporaceae.

The Pythiaceae generally bear their sporangia directly on the somatic hyphae. In some species, the fertile hyphae are no different from the somatic hyphae. The most advanced species of the Pythiaceae produce recognizable sporangiophores, but of indeterminate growth. This means that the sporangiophore continues growing indefinitely, producing sporangia as it grows. The result is the presence of sporangia of different ages—from some that are mature to others that are just being initiated—on the same sporangiophore at any given time.

The Albuginaceae produce short, club-shaped sporangiophores which bear chains of globose sporangia at their tips. As in the Pythiaceae, the sporangiophores are of indeterminate growth. The Albuginaceae are obligate parasites of flowering plants.

The Peronosporaceae, which are probably closely allied to the higher Pythiaceae, bear their sporangia on unmistakable sporangiophores which are characteristically branched. In contrast to those of the higher Pythiaceae, the sporangiophores of the Peronosporaceae are of determinate growth. No sporangia are produced until the sporangiophore completes its development and matures. Then a

single crop of sporangia is produced, all the sporangia being of approximately the same age. After the sporangia fall off, the sporangiophore withers and dies. The type of branching of the sporangiophores of the Peronosporaceae serves as the chief distinguishing feature of the genera in this family. The Peronosporaceae are obligate parasites on plants; no one as yet has succeeded in growing any species on artificial media.

KEY TO THE FAMILIES OF THE ORDER PERONOSPORALES

- A. Sporangiohores similar to the somatic hyphae,
or, if different, then of indeterminate growth *Pythiaceae*
- AA. Sporangiohores strikingly different from the somatic hyphae
 - B. Sporangia in chains at the tips of short,
stout, club-shaped sporangiophores *Albuginaceae*
 - BB. Sporangia borne singly or in clusters, at the
tips of various types of sporangiophores, the
latter of determinate growth *Peronosporaceae*

family PYTHIACEAE

The Pythiaceae include aquatic, amphibious, and terrestrial fungi, many of the last causing serious diseases of economic plants. The mycelium is well developed; haustoria are produced in some species. The hyphae which bear the sporangia are indistinguishable from the mycelium in most species. In some species, however, definite sporangiophores are formed. In such cases the growth of the sporangiophore is indeterminate.

In the most primitive forms the sporangia remain attached to the hyphae which bear them. Upon maturity they produce and liberate a number of zoöspores. In the most advanced species the sporangia are deciduous, and often germinate each by a germ tube instead of producing zoöspores. The type of germination, whether by zoöspores or germ tube, appears to be governed to a great extent by environmental conditions, especially by temperature.

Sexually the Pythiaceae conform to the general pattern described for the Peronosporales as a whole. Oöspores are formed parthenogenetically in some species, but it is probable that fertilization takes place in a large number. Cytological studies are relatively few. On the other hand, the physiology of growth and reproduction in the Pythiaceae has attracted the attention of a number of investigators. Sexuality appears to be relative in some species (Kouyeas, 1953;

Galindo and Gallegly, 1960), and there are indications that a hormonal mechanism, perhaps similar to that in *Achlya*, may be involved in the development of sex organs and oöspores.

The Pythiaceae show a considerable degree of advancement over the Saprolegniaceae, but resemble them sufficiently to have caused some authors¹ in the past to include them with the latter in the Saprolegniales rather than in the Peronosporales. Of interest in this connection are the conclusions of Cantino and Turian (1959) that "nutritional requirements of the Leptomitales and Peronosporales² seem to relate these two orders more closely to one another than to the Saprolegniales."³ At the other extreme, some writers (Wolf and Wolf, 1947) separate the Pythiaceae from both the Saprolegniales and the Peronosporales, elevating them to ordinal rank under the name of Pythiales.

The most common genera of the Pythiaceae are *Pythium* and *Phytophthora*. The first includes some aquatic species parasitic on algae as well as many soil-inhabiting species parasitic on higher plants. The best known of these is *Pythium debaryanum*, the cause of damping-off of seedlings. The genus *Phytophthora* includes many important plant pathogens. Of these, *Phytophthora infestans*, the cause of late blight of potatoes, is the most infamous. When the weather is favorable to the fungus (*i.e.*, when low temperature and high humidity prevail), the disease appears on an epiphytotic scale and, in spite of the control measures that have been worked out, causes damage even in modern times. In former years, the fungus was responsible for the complete destruction of the entire potato crop over large areas. Indeed, the Irish famine of 1845, which was partially responsible for the repeal of the corn laws in England and for a great wave of migration from Ireland to the United States, is directly traceable to *Phytophthora infestans*. The story is related very entertainingly by E. C. Large (1940) in his well-known book, *The Advance of the Fungi*.

genus *PYTHIUM*

Pythium debaryanum will be used to illustrate the general life history of members of the genus *Pythium* (Figure 57). The mycelium, consisting of rather slender, coenocytic hyphae with cellulose walls

¹ Schröter, 1893; Smith, 1938.

² Based on our knowledge of the Pythiaceae alone, inasmuch as the Peronosporaceae and Albuginaceae have not been grown in artificial culture.

³ Quoted by permission of *Review of Microbiology*.

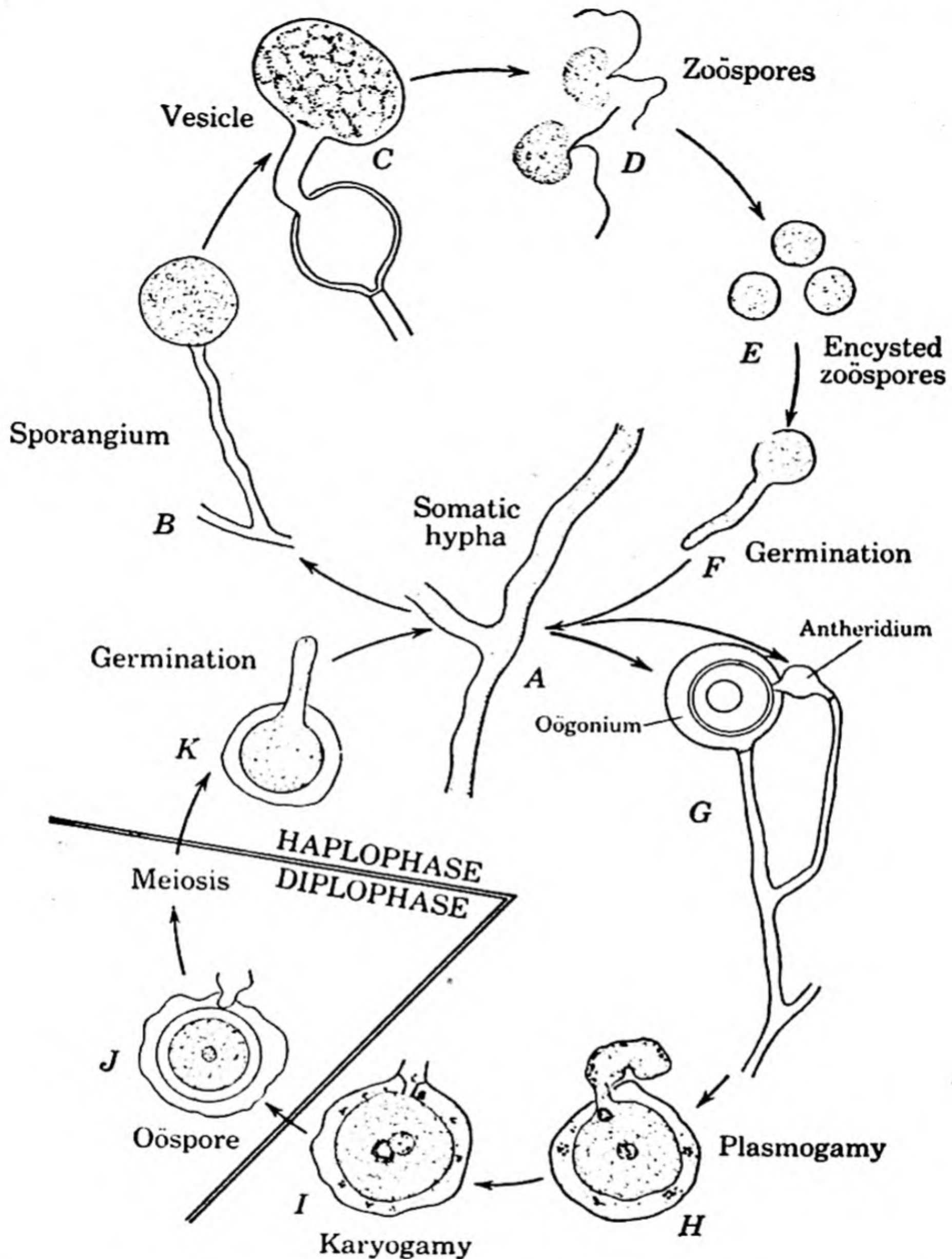


Figure 57. Life cycle of *Pythium debaryanum*. B, G, redrawn from Middleton, 1943, *Mem. Torrey Bot. Club*, 20:1-171; C, redrawn by permission from *Studies on the genus Pythium*, by Velma D. Matthews, 1931, University of North Carolina Press, Chapel Hill; D, F, redrawn by permission from *Elements of plant pathology*, by I. E. Melhus and G. C. Kent, 1939, The Macmillan Company, New York; E, K, constructed; H-J, redrawn from Miyake, 1901, *Ann. Bot.*, 15:653-667.

(Figure 57A), lives in the soil saprobically on dead organic matter or parasitically on the young seedlings of a great many susceptible species of seed plants. The hyphae are both intracellular and intercellular. No haustoria are produced. The sporangia of the organism, constituting the asexual stage, are globose to oval and are either terminal or intercalary on the somatic hyphae (Figure 57B). The sporangia remain attached to the hyphae and germinate in place. Germination is either by zoöspores or by germ tube. Production of zoöspores is preceded by the formation of a bubble-like vesicle at the tip of a long tube which issues from the sporangium. The sporangial protoplast flows into the vesicle through the tube, and differentiation of the zoöspores takes place in the vesicle (Figure 57C).

The formation and liberation of the zoöspores in *Pythium* is a fascinating process to watch under the microscope. The narrow tube which connects the sporangium to the vesicle is well defined, but the vesicular wall is so thin that you need to adjust the microscope mirror very carefully so that the vesicle may be properly illuminated and brought into view. The sporangial protoplast moves rather rapidly through the tube into the vesicle and appears to remain quiescent while the delimitation of the zoöspores is taking place. After some time has elapsed—15 or 20 minutes perhaps—you can detect a slight trembling motion as the crowded zoöspores become restless and begin to move. This motion becomes accelerated, gradually but steadily, until you can see the separate zoöspores moving rapidly within the vesicle, bouncing off their neighbors and the wall of the vesicle. Suddenly the vesicular wall bursts like a soap bubble, and the zoöspores scatter in all directions, dashing out in a rush (Figure 57D).

The zoöspore is kidney-shaped and has two lateral flagella attached on the concave side. After a period of swarming in the film of water present in the soil, the zoöspore comes to rest, encysts, and germinates by a germ tube (Figures 57E, F).

Sexual reproduction in *Pythium debaryanum* has been studied by several investigators. Oögonia and antheridia are developed in close proximity, often on the same hypha, with the antheridium just below the oögonium (Figure 57G). The oögonium is globose with a multinucleate oösphere surrounded by a layer of periplasm. The antheridia are much smaller, and somewhat elongated or club-shaped. Upon gametangial contact, a fertilization tube develops and penetrates the oögonial wall and the periplasm. In the meantime, nuclear division has taken place in both gametangia and all but one functional nucleus in each have disintegrated. The male nucleus now

passes through the tube into the oösphere, approaches the female nucleus, unites with it, and forms the zygote (Figures 57H, I). The oösphere develops into a thick-walled, smooth oöspore which germinates after first undergoing a rest period. At high temperatures (28° C.) the oöspore germinates by germ tube, which develops a mycelium. At lower temperatures (10–17° C.), however, the germ tube stops growing when it has reached a length of 5–20 μ , and the protoplast of the oöspore migrates through the tube, pushes out through the tip, and forms a vesicle in which zoöspores develop (Drechsler, 1952). Meiosis probably occurs in the first divisions of the zygote nucleus (Figures 57J, K).¹

A very large number of species of *Pythium* have been described. *Pythium ultimum* and *Pythium aphanidermatum* are other species, besides *Pythium debaryanum*, which cause damping-off. *Pythium aphanidermatum* is particularly interesting because of its large, irregularly shaped, branched sporangia. For the taxonomy of the genus *Pythium* see Matthews (1931), Middleton (1943), and Sparrow (1960).

genus *PHYTOPHTHORA*

The chief distinction between the genera *Pythium* and *Phytophthora* is the method of sporangial germination. In general, no vesicle is formed in *Phytophthora*, or, if one is formed, the zoöspores differentiate in the sporangium proper and pass into the vesicle as mature zoöspores; they are liberated by the bursting of the vesicular wall. Unfortunately, this distinction does not hold true for all species, and consequently it is very difficult for all but the specialist in the taxonomy of this group of fungi to classify borderline species. Let us look at *Phytophthora infestans*, the notorious cause of potato late blight (Figure 58).

The oöspores of *Phytophthora infestans* appear to be very rare in the eastern hemisphere and in the United States and Canada, and may not in fact play a significant role in the survival of the species. In Mexico, however, oöspores have been found in moderate numbers in potato leaves and may be of considerable importance in the

¹ Mrs. Eva Sansome (1961) reports that meiosis in *Pythium debaryanum* occurs in the gametangia, not in the oöspore. If this is true, the thallus of this organism is diploid and the gametes are the only haploid structures in the entire life cycle. Furthermore, on the basis of subsequent, as yet unpublished, data, Mrs. Sansome concludes (personal communication) that several other Oömycetes she has investigated behave in a similar fashion. This, if confirmed, will change radically our concept of the whole class Oömycetes.

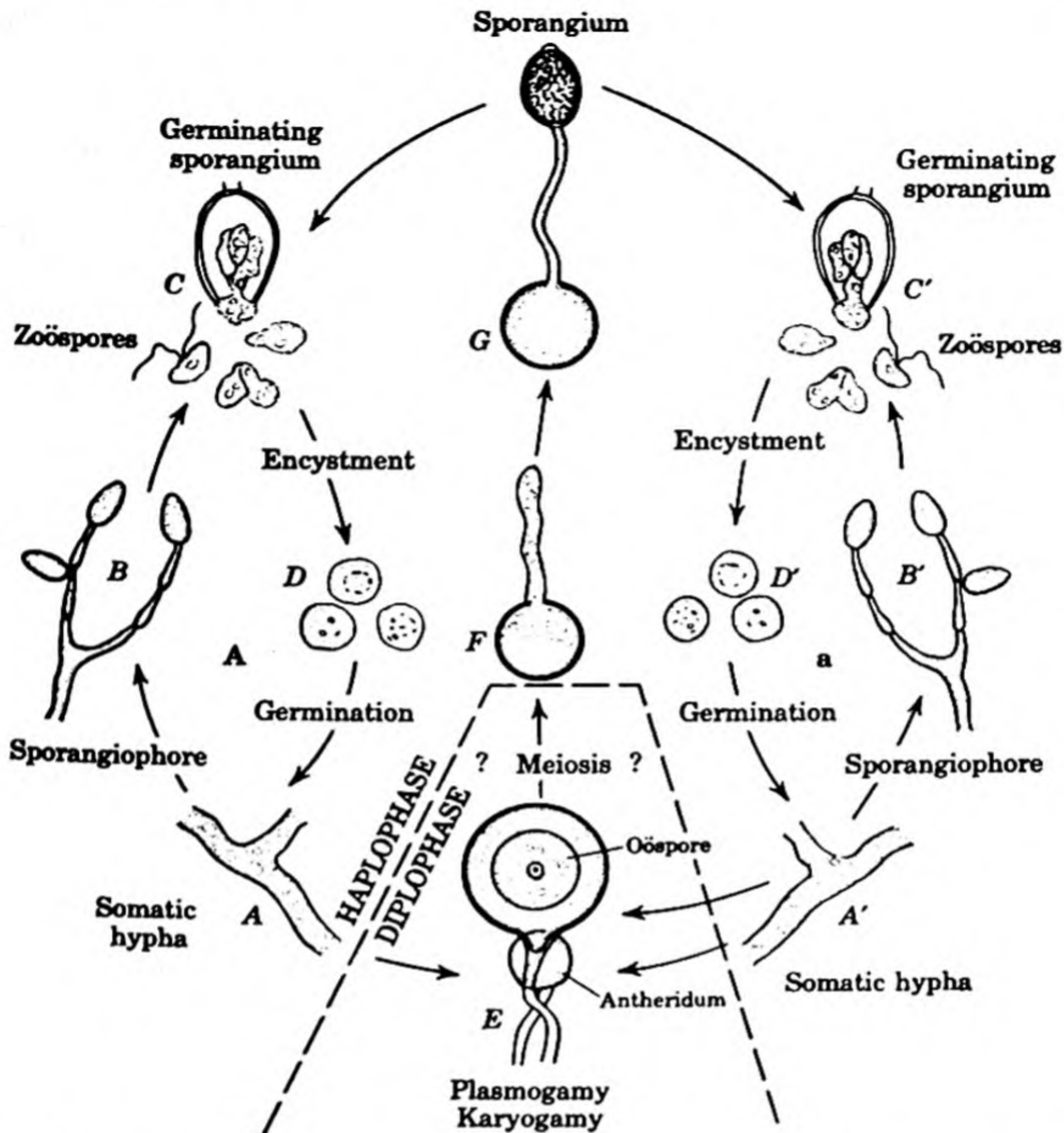


Figure 58. Life cycle of *Phytophthora infestans*. C–D, redrawn from Ward, 1887, *Quart. Jr. Micr. Sci.*, n.s., 27:413–425; E–G, adapted, by permission of the U. S. Army, from photographs in Smoot *et al.*, 1958, *Phytopath.*, 48:165–171.

survival of the organism (Gallegly and Galindo, 1958). It is probable that the same situation exists throughout the Central and South American regions where the potato is native. In most parts of the world, then, *Phytophthora infestans* passes the winter, as a general rule, in the form of mycelium in infected potato tubers (Figure 58A). With the arrival of favorable weather in the spring, the mycelium grows and production of sporangiophores and sporangia begins. Cultural experiments (Crosier, 1934) have shown that 21° C. is the optimum temperature for the growth of the mycelium, but that some growth takes place between 2° and 30°. Above 26° the hyphae die

within a week. Temperature and humidity appear to be the two most important factors determining sporangial production. Abundant sporangial formation takes place in culture between 9° and 22°, but 18–22° is the optimum range. At this range abundant sporangia are produced within 14 hours, whereas at the lower temperatures (9–15°) 48 hours are required. As for relative humidity, 100 per cent is optimum and 91 per cent minimum for sporangial production.

Phytophthora infestans differs from many other members of the family Pythiaceae in that it produces sporangiophores distinguishable from the somatic hyphae. The formation of sporangiophores is an indication of differentiation, and species which possess these structures are considered more advanced than those which produce their sporangia directly on undifferentiated somatic hyphae. The sporangiophores of *Phytophthora infestans* and of other species in the family Pythiaceae are sympodially branched and are of indeterminate growth. The lemon-shaped, papillate sporangia are borne at the tips of the sporangiophore branches (Figures 58B, B'). Apical growth of the sporangiophore continues, however, so that the sporangia actually fall off from a lateral position in this species. The sporangiophore forms a sympodium with a more or less zigzag growth and with characteristic swellings at the nodes. On the potato tuber, the sporangiophores appear in large numbers on cut surfaces, but normally push through the lenticels or injured portions of the skin.

Spring infection of potato plants originates in diseased potato tubers in which the mycelium survives. The fungus grows into the new tissues sprouting from the potatoes and sporulates on the aerial parts of plants. Subsequent infection of potato plants takes place by means of sporangia which are transported by water or are blown by the wind (Hirst and Stedman, 1960). Sporangia of this and other species of *Phytophthora* are extremely susceptible to dessication. When the relative humidity drops much below 100 per cent, the sporangia die in a few hours (Cochrane, 1958). In the presence of water the sporangium germinates either directly by a germ tube which enters through a stoma and infects the leaf, or by means of zoöspores (Figure 58C). Sporangia are capable of germinating within a wide range of temperature from 1.5 to 24° C. However, above 20° the sporangia lose their viability in 1–3 hours in dry air, and in 5–15 hours in moist air. By first exposing sporangia to 40° C., Taylor and his coworkers (1955) greatly increased germination at 20° C. Without pretreatment, 9 per cent of the sporangia germi-

nated after 12 hours, whereas, after 5 minutes' exposure to 40°, 49 per cent germinated in the same period of time.

Other factors besides temperature and moisture, such as age of sporangia, also affect germination. The method of germination is largely governed by temperature. Low temperatures favor zoöspore production; higher temperatures, germ tube production. The optimum temperature for direct (germ tube) germination is 24° C., whereas that for indirect germination is 12° C. Zoöspores swim in the film of water for 15 minutes at high temperature and up to 24 hours as the temperature decreases. Eventually they come to rest, encyst, and germinate each by a germ tube. The germ tube produces an **appressorium** (pl. **appressoria**; L. *apprimere* = to press against), a flattened, hyphal, pressing organ, from which a minute infection peg grows and enters the epidermal cell of the host (Pristou and Gallegly, 1954). If conditions favorable to penetration of the host last for 10 hours, a high degree of infection may be expected.

After penetrating into the leaf, the germ tube develops into a profusely branched mycelium which is intercellular, sending long, curled haustoria into the leaf cells. A few days after infection, if the weather is favorable, numerous sporangiophores emerge from the stomata of the potato leaves and give rise to large numbers of sporangia. These are spread by the wind and infect new plants. A large number of asexual generations are thus produced in one growing season if conditions favor the development of the fungus.

The first authentic report of the discovery of a sexual stage for *Phytophthora infestans* was published by Clinton in 1911. Clinton found the oöspores in pure cultures of this organism. Later experimental work has shown that the fungus is heterothallic, *i.e.*, requires two mating types for sexual reproduction. These observations (Smoot *et al.*, 1958; Gallegly and Galindo, 1958; Galindo and Gallegly, 1960) have explained why oöspores are rare in most parts of the world but occur in fair numbers in Mexico. Whereas both mating types occur in a 1:1 ratio in Mexico, a large number of isolates from the United States, Canada, western Europe, South Africa, and the West Indies all belong to a single mating type. In the absence or rarity of the second mating type, oöspores are produced very infrequently. Sexual reproduction takes place by means of antheridia and oögonia of opposite mating types. While still in the process of development, the antheridium is punctured by the oögonium, which grows through it and develops into a globose structure above the antheridium (Pethybridge and Murphy, 1913). The mature antheridium thus forms a funnel-shaped collar around the base of the

mature oögonium (Figure 58E). Fertilization has not been observed but is presumed to take place, although it is known that in this species oöspores can develop parthenogenetically in the absence of an antheridium. Oöspores (Figure 58F) germinate by means of a germ tube which usually terminates in a sporangium (Figure 58G). At times, however, the germ tube will proceed to produce mycelium. Where meiosis takes place is not known; but, if the organism follows the regular pattern, meiosis would be expected to take place in the oöspore at the time of germination. Mating type should segregate at this point in the life cycle.

family PERONOSPORACEAE

This is the most highly advanced of the three families of the order Peronosporales. All species in this family are obligate parasites of vascular plants, causing diseases called downy mildews. Economically they are among the most important fungi. Their hosts include a large number of plant families, many of them widely distributed and widely cultivated commercially. Diseases caused by the Peronosporaceae include, among many others, the downy mildews of grape caused by *Plasmopara viticola*, of onion caused by *Peronospora destructor*, of lettuce caused by *Bremia lactucae*, of cucurbits caused by *Pseudoperonospora cubensis*, and of various grasses caused by *Sclerospora graminicola*.

Plasmopara viticola has as interesting a history as *Phytophthora infestans*. The story has been told many times and in various editions, but it always bears repetition for the benefit of those who have not heard it. *Plasmopara viticola* is a fungus native to North America. It has probably been attacking for thousands of years the grapes native to this continent, during which time natural selection, operating as usual, has produced a balance of power between the parasite and the host so that *Plasmopara viticola* can live on the wild American grape without the latter's being seriously affected by it.

The same balance exists between the American grape and the *Phylloxera*, a root aphid also native to this continent. Somehow, about 1865, *Phylloxera* was introduced into France. The European grape (*Vitis vinifera*), not having had the opportunity to evolve along anti-*Phylloxera* lines, was extremely susceptible. With millions of Frenchmen depending on the grape industry for a living, this was no small matter. The problem was eventually solved by the importation of resistant American stock and the grafting of the *vinifera* grape thereon.

Now it seems, although no one knows for certain, that some of the American vines imported into France to combat *Phylloxera* carried mycelium or oöspores of *Plasmopara viticola*, and, just as the French were beginning to enjoy their wine again, the new pest struck the very susceptible leaves and fruits of the *vinifera* grapes. In dry years this was not too serious, but in wet years it was disastrous. I have personally seen unsprayed European vineyards in which the crop was *completely* destroyed by this fungus. In the late eighteen seventies, all vineyards were unsprayed because fungicides were unknown. The French grape and wine industry seemed doomed.

One day in 1882, so the story goes (Large, 1940), Alexis Millardet, professor at the University of Bordeaux, was passing by a vineyard, thinking no doubt about his fungi, when he noticed that the vines bordering his path looked much healthier than those beyond them, which showed the now too familiar symptoms of downy mildew. He noticed further that the outside row appeared to have been sprayed with some substance of poisonous appearance. His curiosity aroused, he made inquiries which revealed that the owner had poisoned the vines along the walk with a mixture of copper sulphate and lime to discourage strangers from picking his grapes. Millardet returned to his laboratory and started to work on this clue, from which he soon developed Bordeaux mixture, the first fungicide to be used in the control of plant disease.

The story has a sequel. While the French were worrying about the *Phylloxera* and the mildew, some Mediterranean countries, believing the French grape and wine industries doomed, entered upon an unprecedented program of grape planting. When the American stocks solved the *Phylloxera* problem and Bordeaux mixture controlled downy mildew effectively, overproduction of grapes created an economic crisis in these countries.

The Peronosporaceae include a number of common genera differentiated chiefly by the branching of their sporangiophores (Figure 59). Whereas only a few of the Pythiaceae have a differentiated sporangiophore, all the Peronosporaceae bear their sporangia on sporangiophores. In *Basidiophora* the sporangiophore is club-shaped with a swollen head over which the sporangia are borne on minute sterigmata. In *Sclerospora* the sporangiophore is a long, stout hypha, with many upright branches near the end, bearing sporangia at the tips. In *Plasmopara* the branches and their subdivisions occur typically at right angles and are irregularly spaced. In *Peronospora* and *Pseudoperonospora* the sporangiophores are dichotomously branched at acute angles and taper to gracefully curved pointed tips on which

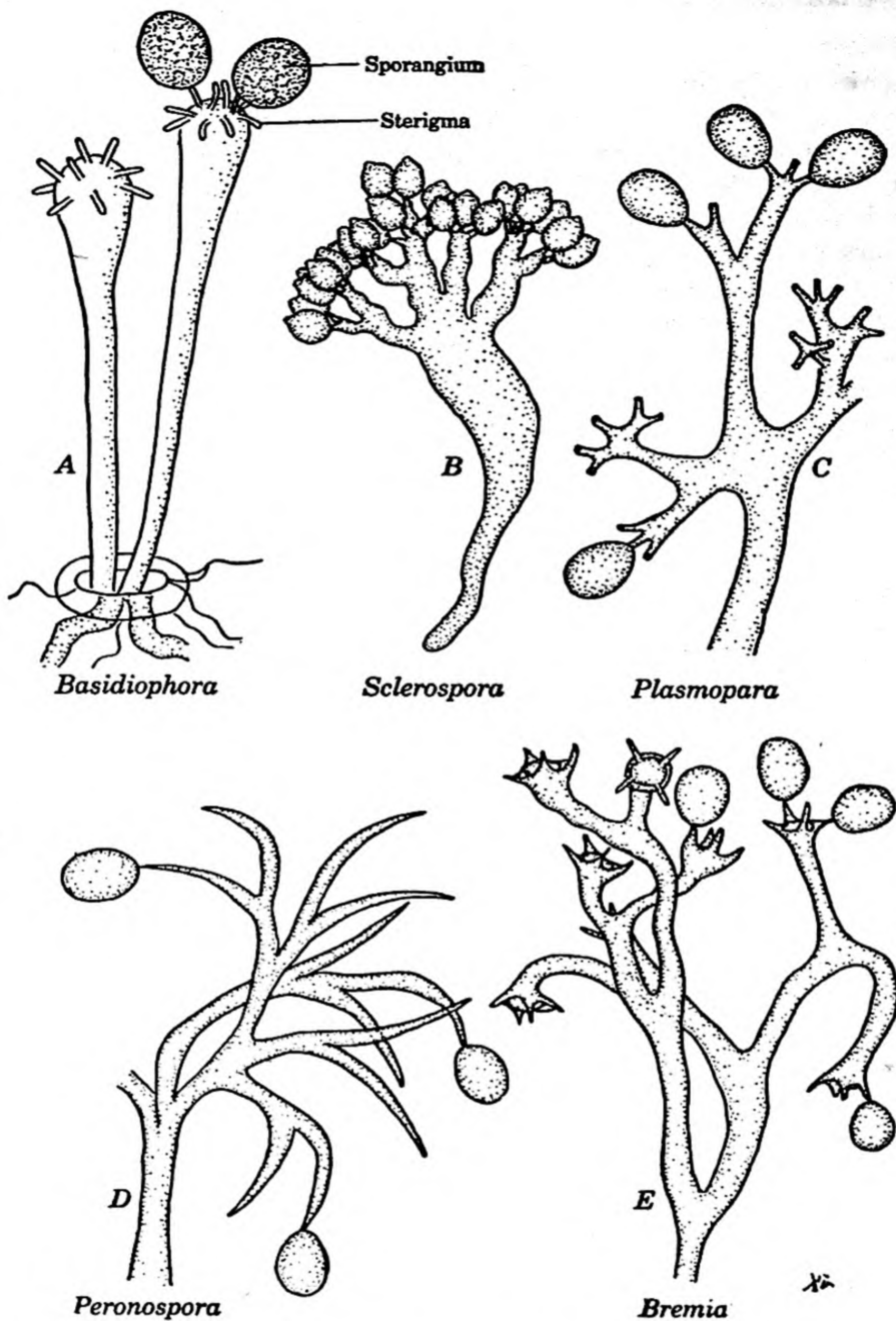


Figure 59. Sporangiophores characteristic of five genera of the Peronosporaceae. A, redrawn from Cornu, by permission, from the *Lower fungi—Phycomycetes*, by H. M. Fitzpatrick, 1930, McGraw-Hill Book Co., New York; B, redrawn from Weston, 1924, *Jr. Agr. Res.*, 27:771-784.

sporangia are borne.¹ *Bremia* is similar to *Peronospora* except that the tips of the branches are expanded into saucer-shaped structures with four sterigmata each along their margin bearing the sporangia.

The sporangiophores of the Peronosporaceae have a determinate growth as contrasted to the indeterminate growth of the sporangiophores of the higher Pythiaceae. In the Peronosporaceae, the mycelium produces a sporangiophore which reaches maturity, stops growing, and then produces a crop of sporangia on sterigmata at the apices of its branches. All the sporangia are therefore of approximately the same age. They are round, oval, or lemon-shaped, and, without exception, deciduous and wind-disseminated.

In most genera of the Peronosporaceae, the sporangia germinate by zoöspores or germ tubes, depending on environmental conditions, but the sporangia of *Peronospora* invariably germinate by means of germ tubes. Such sporangia are considered spores in themselves and are often termed conidia. Conidia always germinate by germ tubes. Conidia, which are particularly characteristic of the Ascomycetes, are also found in some of the lower fungi (Oömycetes, Zygomycetes, Trichomycetes), in which they represent the final stage in the evolution of the sporangia. Although mycologists generally use the term sporangia to indicate these structures in all the Peronosporales, plant pathologists prefer to apply the term conidia to the deciduous sporangia. It really does not matter what term you use so long as you understand the development and the function of the structures concerned. Here again we have a question of a man-made definition and a man-created border line which fungal sporangia—or are they conidia?—will continue to defy.

The oöspores of the Peronosporaceae as a general rule germinate by germ tubes. Those of *Peronospora tabacina* appear to be an exception. According to Person and Lucas (1953), they produce a sporangial vesicle which releases zoöspores.

The life histories of all species in this family follow the same general pattern, which is similar to that of *Pythium* and *Phytophthora*, explained in detail a few pages back. The life history of *Plasmopara viticola* is illustrated in Figure 60.

family ALBUGINACEAE

The Albuginaceae include the fungi known as white rusts. All of them are obligate parasites causing diseases of vascular plants.

¹ The sporangia of *Pseudoperonospora* germinate typically by zoöspores, whereas those of *Peronospora* always germinate by germ tube.

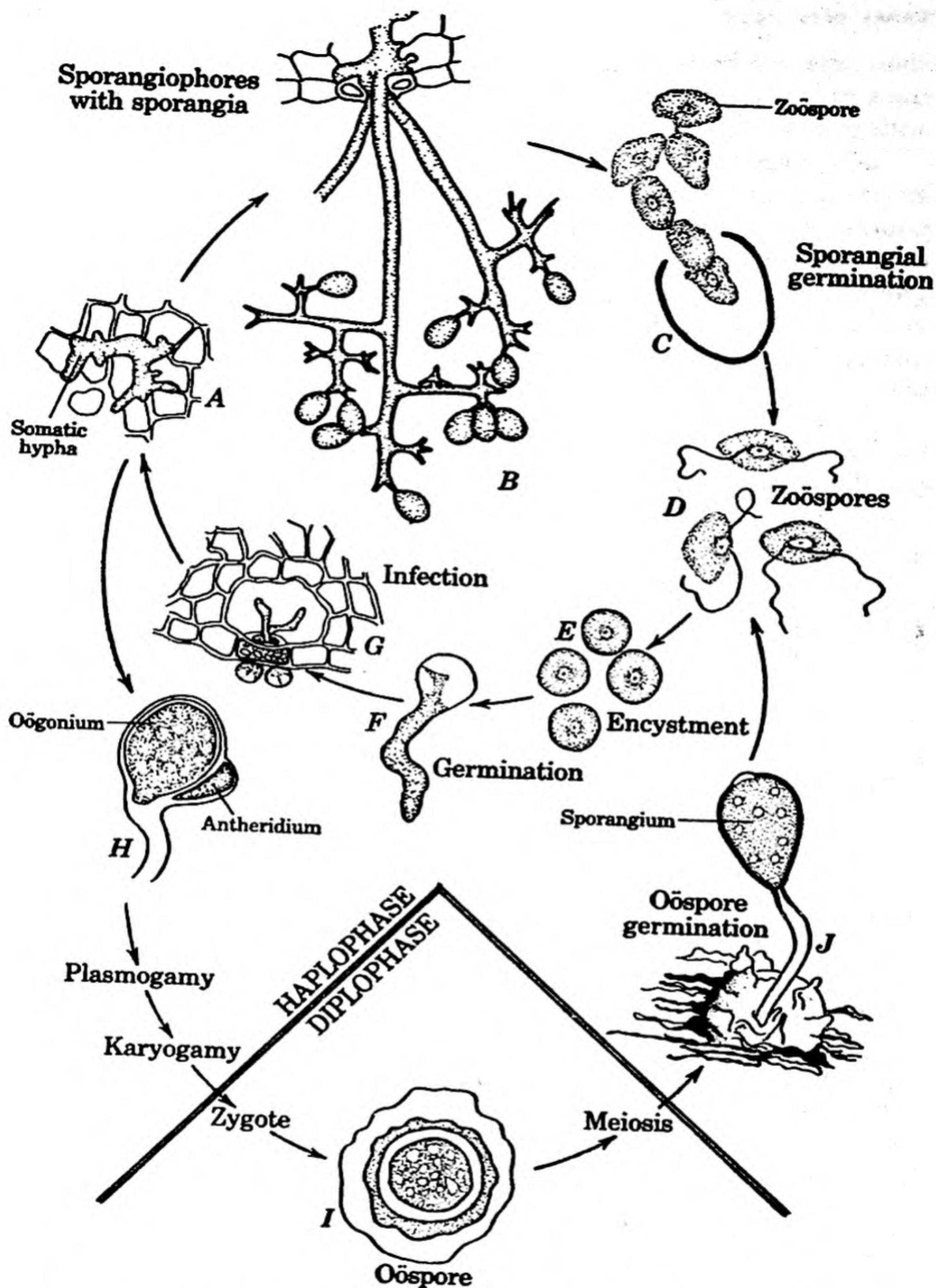


Figure 60. Life cycle of *Plasmopara viticola*. C-G, I, J, redrawn from Gregory, 1912, *Phytopath.*, 2:235-249; H, redrawn from Millardet, in Engler and Prantl, 1897, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^o, Wilhelm Engelmann, Leipzig.

There are several species of *Albugo*, the only genus in this family. Of these, *Albugo candida*, which attacks crucifers, is the only one causing disease attaining economically significant proportions. An outbreak of white rust on horse-radish or on cabbage, for example, sometimes causes considerable damage. Some of the other species commonly found are *Albugo ipomoeae-panduranae* on sweet potato and morning glory, *Albugo portulacae* on *Portulaca*, *Albugo occidentalis* on spinach, and *Albugo bliti* on various members of the *Amaranthaceae*.

Life History. In *Albugo candida* (Figure 61) the mycelium is intercellular and feeds by means of haustoria which penetrate the host cell walls through minute perforations, and expand on the inside of the cells into globose or knob-like structures (Figure 61A). The mycelium grows and ramifies, and, when a certain stage of maturity is reached, produces short, club-shaped sporangiophores from the tips of a large number of hyphal branches in one locality. The sporangiophores are borne in close proximity to one another in solid layers or beds immediately below the epidermis of the host. When the sporangiophores reach a certain stage of growth, they begin to cut off a number of sporangia at their tips. Each sporangiophore gives rise to several sporangia which it produces in succession, one below the other, so that a chain of sporangia is formed with the oldest at the tip of the chain and the youngest at the base (Figure 61B). As the sporangia mature, they become detached and are freed in the space between the sporangiophores and the epidermis of the host. Both the growth of the fungus and the production of numerous sporangia exert a pressure from below on the host epidermis, causing it to bulge and eventually to burst over the growing sorus. Upon the bursting of the epidermis, the sporangia are released and form a white crust on the surface of the host. Individually the sporangia are normally globose, but pressure during their formation results in flattened sides so that some of them are cuboid or polyhedral. They have rather thin walls and are filled with protoplasm. The sporangia are multinucleate. Disseminated by the wind, by water, and perhaps by other agents as well, a great percentage of them perish, never reaching a susceptible host. The sporangia of *Albugo* germinate by zoöspores or by germ tubes, depending on the temperature. When zoöspores are produced, the sporangia extrude four to twelve zoöspores in an advanced stage of differentiation, into a sessile vesicle (Vanterpool, 1959). Subsequent details of the asexual cycle follow the pattern typical of the *Peronosporales* (Figures 61C–G).

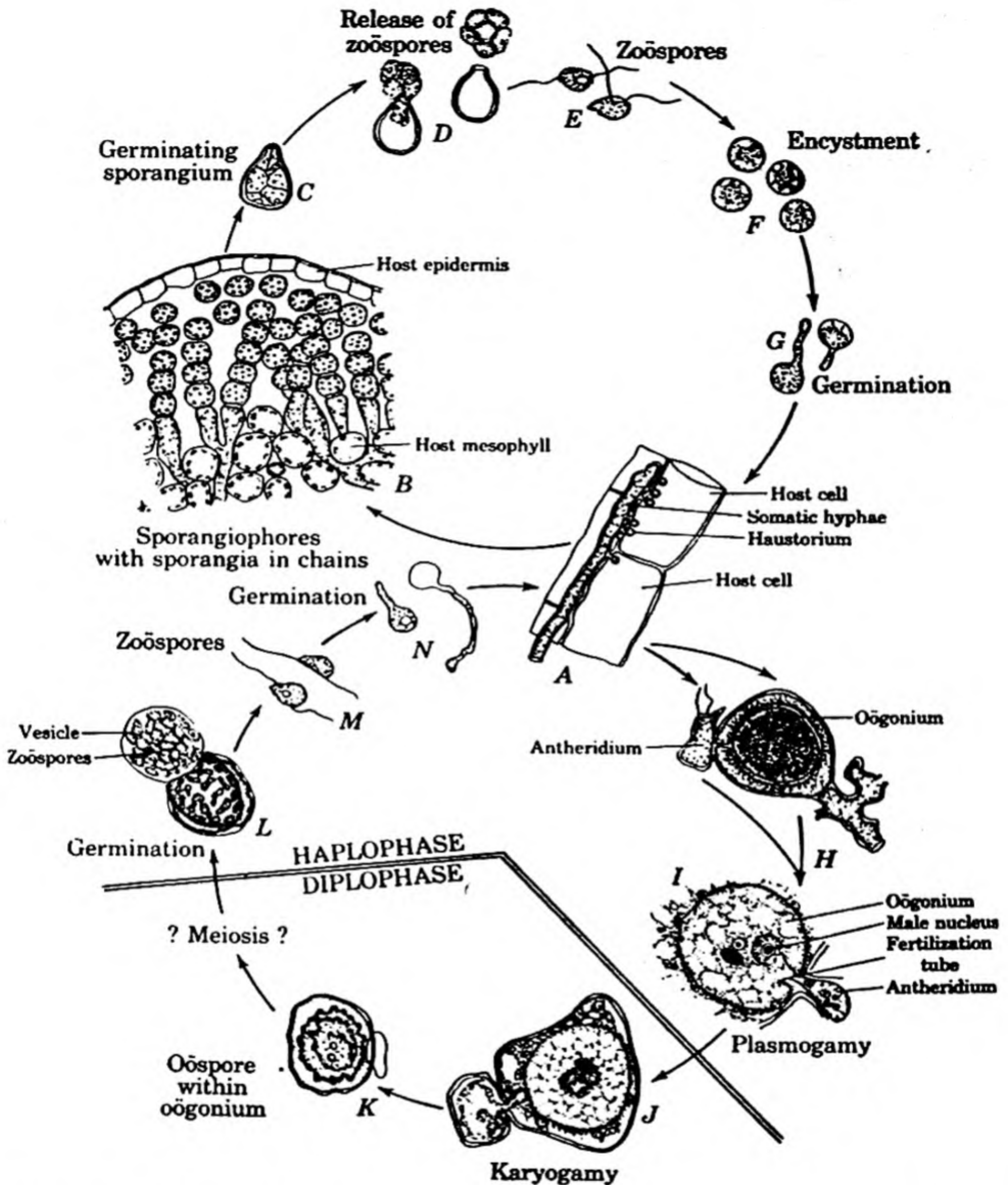


Figure 61. Life cycle of *Albugo candida*. A, C-H, K-N, redrawn from De Bary, 1863, *Ann. sci. nat. Bot.*, 4 ser., 20:5-148; I, J, redrawn from Davis, 1900, *Bot. Gaz.*, 29:297-311, by permission of University of Chicago Press, Chicago.

Sexual reproduction in its gross aspects is similar in all species, but the cytological details of fertilization seem to fall into at least three patterns. The following discussion will be confined to only one of these patterns and applies specifically to *Albugo candida*. Oögonia and antheridia are formed within the tissues of the host (Figure 61H). Both organs are multinucleate at the start, but only one nucleus in each is finally functional. The gametangia are formed near each other and are borne terminally on somatic hyphae. They soon establish contact, the antheridium contacting the oögonium at the side. When mature, the globose oögonium contains an oösphere surrounded by periplasm. Its functional egg nucleus is drawn near the center of the oösphere while the other nuclei move into the periplasm. The antheridium now forms a fertilization tube; a single male nucleus passes through it together with some cytoplasm, approaches the egg nucleus, and fuses with it (Figures 61I, J). The resulting zygote nucleus divides several times while the fertilized oösphere is being transformed into an oöspore by the development of a thick wall (Figure 61K). The oöspore wall of *Albugo candida* is warty. Oöspores of some species have a network of ridges over the surface. The character of the oöspore is a useful criterion in distinguishing between species of *Albugo* (Figure 62).

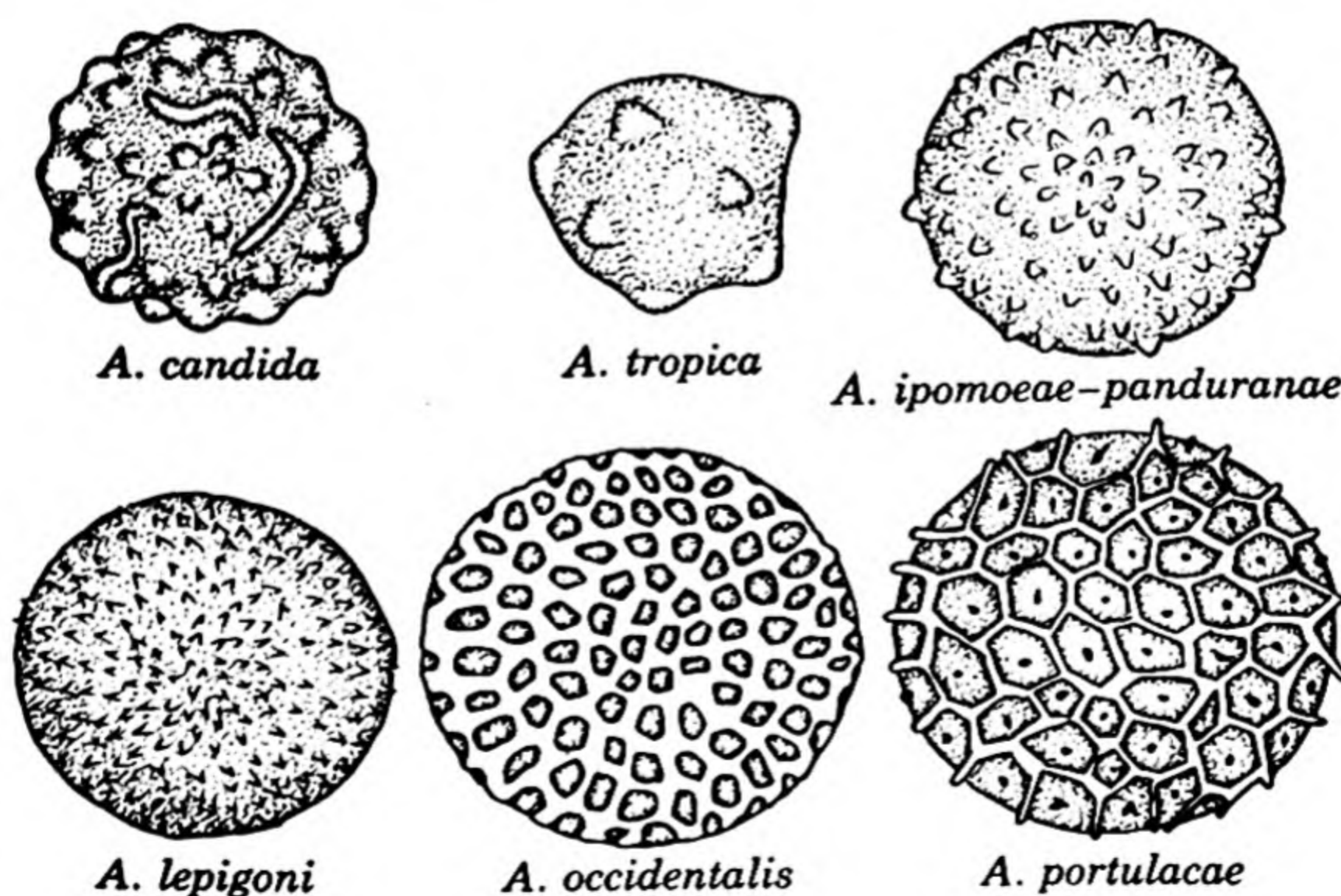


Figure 62. Oöspores of six species of *Albugo*. Redrawn from Wilson, 1907, *Bull. Torrey Bot. Club*, 34:61-84.

After several divisions of the zygote nucleus, two of which are meiotic, the oöspore enters a resting stage. The following spring the nuclei resume their mitotic activity, and the protoplast of the oöspore eventually divides into a large number of uninucleate sections, each of which develops into a biflagellate, reniform zoöspore. An oöspore germinates in one of two ways (Vanterpool, 1959). Either it extrudes its zoöspores into a sessile vesicle, or it forms a short exit tube which terminates in a vesicle. Each oöspore produces from forty to sixty zoöspores. Oöspores apparently never germinate directly by germ tubes as do those of *Phytophthora infestans*, for example. The oöspore thus behaves like a resting sporangium. When the vesicle wall bursts, the zoöspores are liberated; they swarm, encyst, and finally germinate by germ tubes which infect the host (Figures 61L-N).

In species attacking perennial hosts, the mycelium is capable of overwintering in the infected tissues. Remaining dormant during the winter, it resumes activity in the spring and grows into the new shoots which the host produces. Infection, in such cases, is said to be systemic.

Biological Specialization. We have seen that both the Peronosporaceae and the Albuginaceae are obligate parasites of vascular plants. Species are distinguished on the basis of their morphology, *i.e.*, size of sporangia, sculpturing of oöspore wall, etc. Each species is capable of infecting a certain group of closely related host plants. For example, *Albugo candida* infects members of the family Cruciferae, but no plants outside this family, at least in North America. Wilson (1907), who examined a great many collections of this fungus, stated that there is a "remarkable stability of essential characters" in this species in spite of the fact that it attacks so many different hosts. *Albugo candida* is therefore a good morphological species. Within this morphological species, however—and this is important—cross-inoculation from one species of host to another will not always result in infection. This is interpreted to mean that the species *Albugo candida* is composed of a number of biological forms which are morphologically identical, but differ in their ability to infect various crucifers. These biological forms or strains are, therefore, specialized in their parasitism, and the phenomenon is known as biological specialization.

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8 class PLASMODIOPHOROMYCETES the endoparasitic slime molds

General Characteristics. The Plasmodiophoromycetes are obligate endoparasites of vascular plants, algae and fungi, which usually cause an abnormal enlargement of the host cells, called **hypertrophy** (Gr. *hyper* = over + *trophe* = food). The result is the enlargement of the infected portions of the host and, in higher plants, the disruption of the vascular elements. In the latter event, the general stunting and premature death of the host occur.

The somatic phase of the Plasmodiophoromycetes is a plasmodium which develops within the host cells. Plasmodia give rise to zoösporangia containing zoöspores, or directly to resting spores which are produced by cleavage of the plasmodium into uninucleate portions. No fructifications are formed, but the spores in some genera are united and form spore balls or discs. Upon germination, each resting spore releases a single swarm cell. Both swarm cells and zoöspores bear two unequal, anterior flagella, both of the whiplash type. Work by Kole and Gielink (1961, 1962) on this point is very convincing. The electron micrograph in Figure 63 is theirs.

Nuclear division at some stages of the life cycle of the Plasmodiophoromycetes is of a type found in no other fungi, but known to occur in the Protozoa. During division, an intranuclear spindle is formed on which the chromosomes are arranged in a ring around the nucleolus. As the chromosomes split, a ring of chromosomes passes to each pole. The nucleolus elongates, becomes dumbbell-shaped, and divides into two portions which form the nucleoli of the two daughter nuclei. The dumbbell-shaped nucleolus surrounded by a chromatin ring appears like a cross when viewed from the side, hence the name **cruciform** (L. *crux* = cross) given to this type of division.

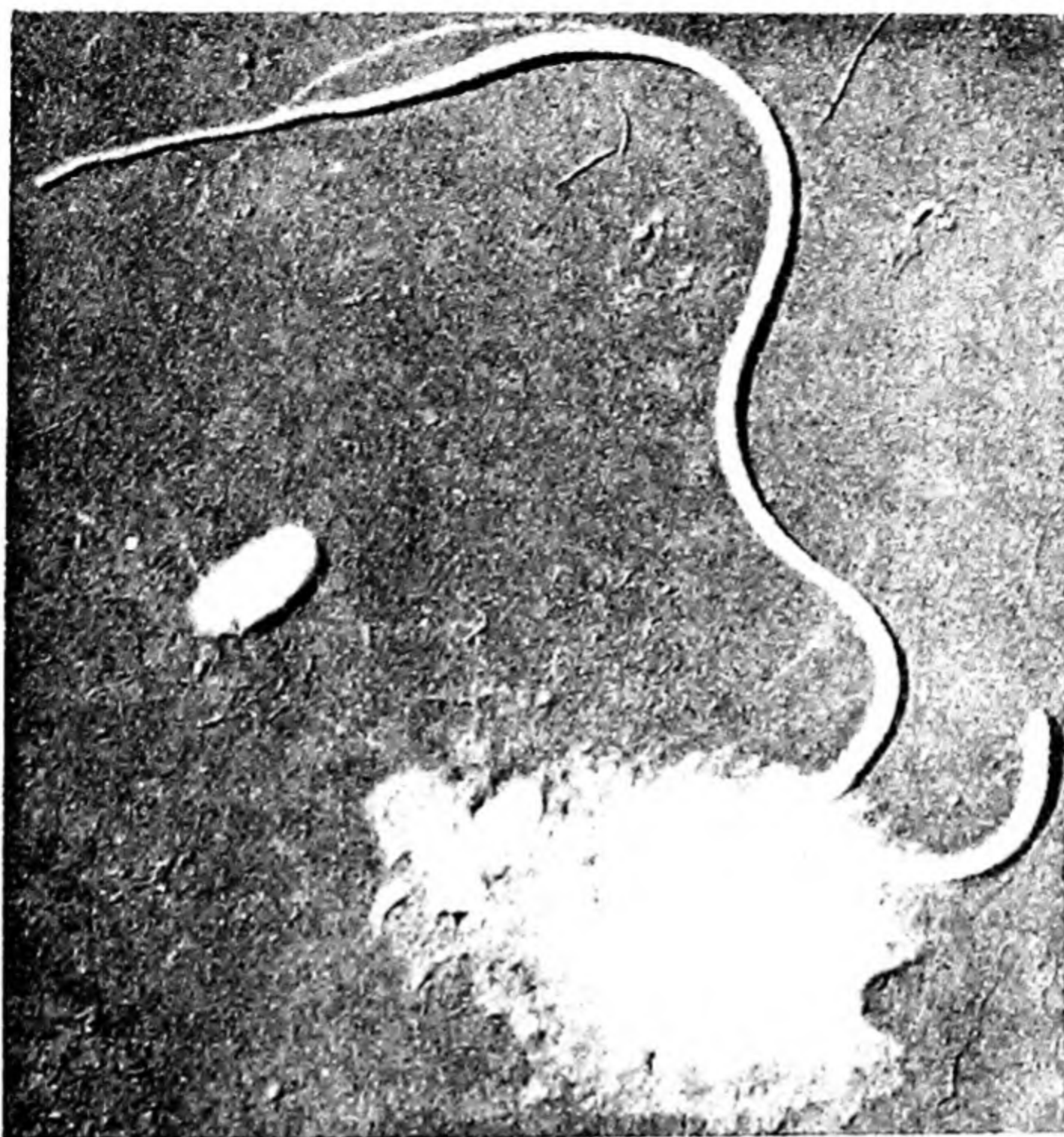


Figure 63. *Plasmodiophora brassicae*. Electron micrograph of a swarm cell which has issued from a resting spore. Two unequal flagella, the short one with a blunt end, the long one with a pointed end, are clearly evident. Approx. $\times 9000$. Courtesy Kole and Gielink, 1962, *Konkl. Nederl. Akad. Wetensch. Proc.*, ser. C, 65:117-121, by permission of the Royal Dutch Academy.

Another interesting phenomenon which has been described as occurring in the Plasmodiophoromycetes is the so-called **akaryote phase** (Gr. *a* = not + *karyon* = nut, nucleus). This is a stage in which the nuclear body seems to disappear, most of the chromatin failing to take the usual stain. Whether this is a true phase through which the nuclei of these organisms pass or whether it is an artifact due to improper staining is still a matter of considerable controversy (Miller, 1958).

Occurrence, and Importance to Man. The occurrence and geographic distribution of the Plasmodiophoromycetes obviously coincide with those of their hosts. Many species parasitize freshwater algae such as *Vaucheria*, or aquatic fungi such as *Saprolegnia*,

Achlya, and *Pythium*. Other species parasitize aquatic and marsh vascular plants in the genera *Isoetes*, *Halophila*, *Zostera*, *Juncus*, etc., or land plants, such as cabbage, potato, *Nasturtium*, and *Veronica*.

There are only two species which are of economic importance: *Plasmodiophora brassicae* is the widespread cause of clubroot or finger-and-toe disease of cabbage and related plants, both cultivated and wild, and *Spongospora subterranea* is the causal agent of powdery scab of potatoes. Its special form *Spongospora subterranea* f. sp. *nasturtii* causes a serious disease of water cress.

General Life Cycle. In spite of a number of critical studies on various members of this class, no general life cycle pattern for the Plasmodiophoromycetes has emerged as yet. Resting spores, swarm cells, plasmodia, and zoösporangia with zoöspores appear to occur in most species. The great controversy hinges on the occurrence of a sexual stage and the alternation of a haploid with a diploid cycle. A discussion of some points in the general life cycle which need clarification follows.

The resting spores germinate, each releasing a swarm cell. Swarm cells are believed to penetrate into the host cells as uninucleate amoebae and there to develop into plasmodia. However, because it is difficult to make continuous observations over a long period of time, even when the material is favorable, the evidence for this method of plasmodial formation is all circumstantial. If plasmodia develop in this manner, they are probably haploid. Nuclear division in the plasmodia is cruciform. After the plasmodium reaches a certain size, determined to a great extent by the size of the host cell, it cleaves into usually multinucleate portions, each of which becomes surrounded by a membrane and develops into a zoösporangium. Zoöspores are released outside the host through exit papillae on the sporangia and through pores dissolved in the host wall. What happens next is a matter of controversy. Whether zoöspores reinfect the host and repeat the life cycle, or whether they act as planogametes, fuse in pairs, and infect the host as zygotes, needs to be clarified.

Some plasmodia, instead of developing into zoösporangia, cleave into uninucleate portions which secrete cell walls and become resting spores. These plasmodia are indistinguishable from those which produce zoösporangia until cleavage occurs. What is the difference between these two types of plasmodia? Some mycologists believe that plasmodia which develop during early infection produce zoösporangia, whereas those which develop later produce resting spores.

Does the environment then govern the type of structure which the plasmodia will produce? Other mycologists believe that the plasmodia which form zoösporangia are haploid, whereas those which form resting spores are diploid. If this is true, the diploid plasmodia probably originate by growth and nuclear division of a zygote, as in the Myxomycetes. This presupposes a fusion of cells somewhere in the life cycle. Such fusions have been observed in both *Plasmodiophora brassicae* and *Spongospora subterranea* (Kole, 1954, 1955), but no karyogamy has been seen. This does not mean that it does not occur! If diploid plasmodia are responsible for the production of the resting spores, it is probable that meiosis occurs before spore

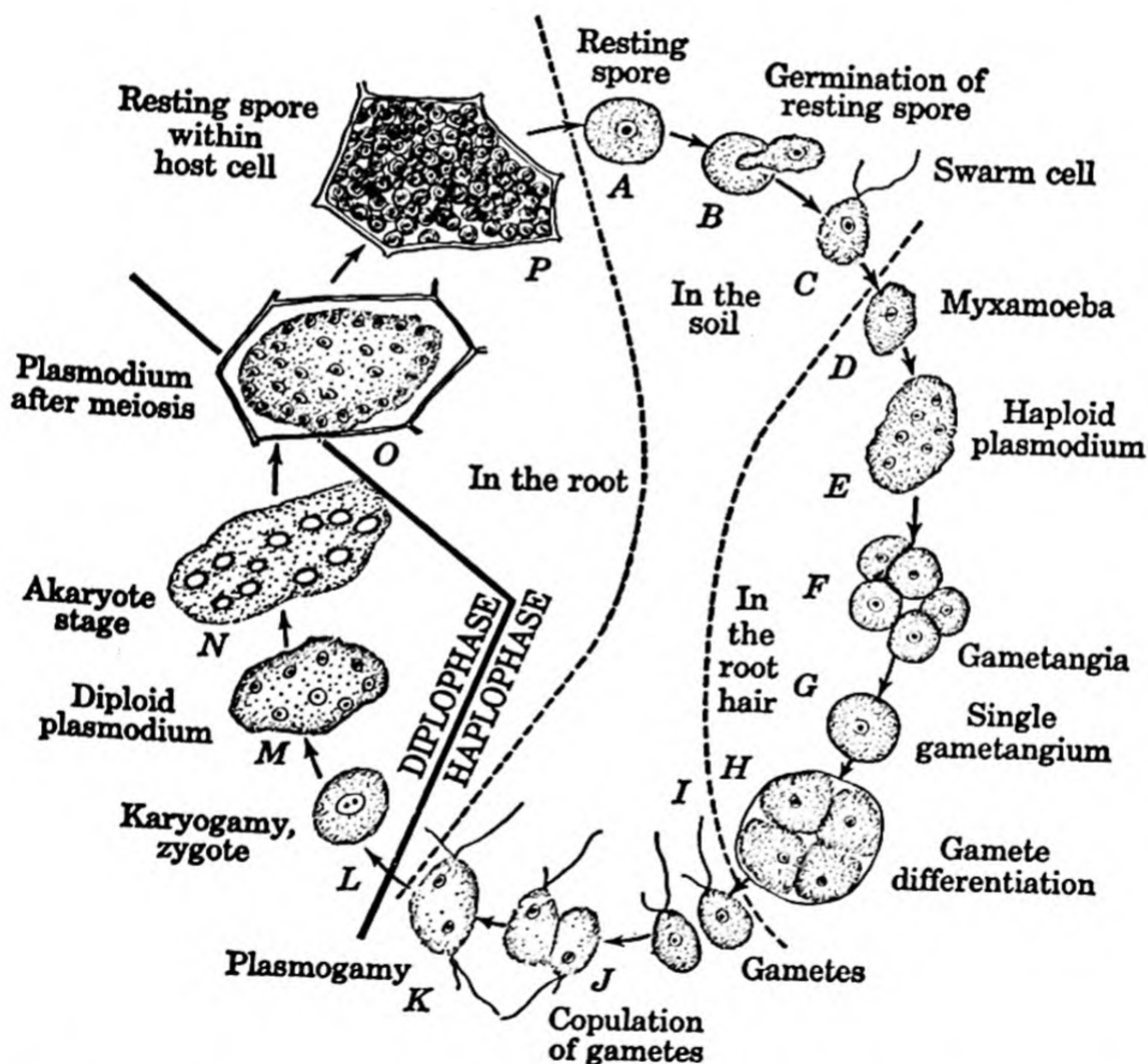


Figure 64. Diagrammatic presentation of the possible sequence of events in the life cycle of *Plasmodiophora brassicae*. By permission of the author, based on Karling, 1942, *The Plasmodiophorales*, published by the author, New York.

formation. This also has been claimed for *Spongospora subterranea*, but chromosome counts—the only positive way to prove meiosis—are so difficult to make in these fungi that no one is sure that meiosis indeed occurs.

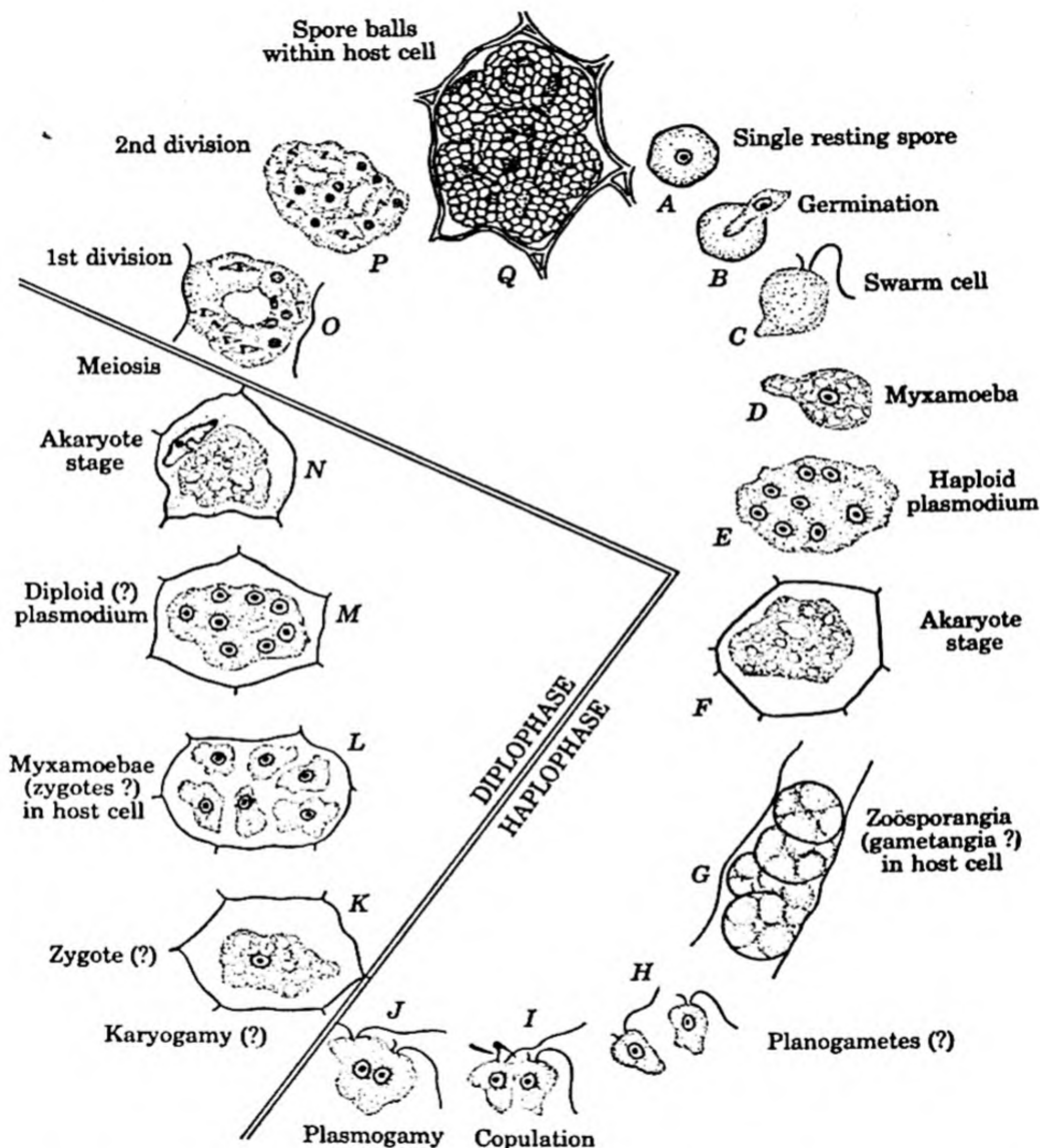


Figure 65. Diagrammatic representation of the possible sequence of events in the life cycle of *Spongospora subterranea*. C, G, redrawn by permission of Macmillan and Co., London, from Ledingham, 1934, *Nature*, 133:534, 135:394; D, redrawn from Cook, 1933, *Arch. Protistenk.*, 80:179–254; K–N, redrawn from Osborn, 1911, *Ann. Bot.*, 25:327–341.

Figures 64 and 65 represent our present thinking on the life cycles of *Plasmodiophora brassicae* and *Spongospora subterranea*. They are based on a number of research papers listed at the end of this chapter.

Classification. The Plasmodiophoromycetes comprise a single order, the Plasmodiophorales, with but a single family, the Plasmodiophoraceae. In possessing a plasmodium, and in their type of motile cells, they resemble the Myxomycetes, with which they have often been grouped. They differ from the Myxomycetes in their biology, in their zoösporangial stage, in that they form no fruiting bodies when the resting spores are produced, and in that the spore walls apparently contain no cellulose. If their plasmodia are indeed haploid, this would constitute another important difference. Because of these reasons, many authors have included them in the Phycomycetes, in the wide sense (see page 184), or in the Archimycetes, a class of lower fungi in which some authors place the non-mycelial, sporangial fungi. Sparrow (1958/1959), recognizing that the Plasmodiophorales have probably originated independently of the groups with which they were formerly affiliated, separated them from the other classes of fungi and designated them as Plasmodiophoromycetes. In the present state of our ignorance concerning them, this treatment appears to be justified and has been adopted here.

We recognize nine genera in the Plasmodiophoraceae. These are separated currently on the basis of the arrangement of the resting spores, even though serious doubts have been expressed about the reliability of such distinctions (Palm and Burk, 1933). These genera are *Plasmodiophora*, *Spongospora*, *Sorodiscus*, *Sorosphaera*, *Ligniera*, *Tetramyxa*, *Octomyxa*, *Polymyxa*, and *Woronina*. A few other genera have also been described, but their validity, or their inclusion in this family is questionable.

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9 class ZYGOMYCETES bread molds, fly fungi, and animal traps

Introduction. In the early days of mycology the large and heterogeneous class Phycomycetes was subdivided into two sub-classes: the Oömycetes, in many of which the resting spore or sporangium develops from the fertilized egg, and the Zygomycetes, in which the resting spore develops from the fusion of two usually equal gametangia. Whereas the Zygomycetes were recognized as a unified, more or less well-limited group, it became more and more evident as our knowledge of the Oömycetes expanded that this was an artificial conglomeration of unrelated forms. When Sparrow, in 1943, broke away from the oömycete concept and emphasized flagellation as the important phylogenetic and taxonomic criterion, he placed the fungi formerly called Oömycetes into two large series: the Uniflagellatae and the Biflagellatae, treating the Hyphochytriales as a separate order not belonging to either series. Inasmuch as his book dealt only with aquatic Phycomycetes, he did not include in his classification the Zygomycetes, which are almost strictly terrestrial fungi.

Other authors, accepting Sparrow's classification but wishing to deal with all major groups of fungi, divided the Phycomycetes into three series: the Uniflagellatae, the Biflagellatae, and, for the sake of uniformity of concept, the Aplanatae (Alexopoulos, 1952) or Aflagellatae (Smith, 1955). In his 1958 address to the Mycological Society of America, later published in *Mycologia*, Sparrow recognized four "galaxies" of aquatic Phycomycetes and gave them the class names Chytridiomycetes, Hyphochytridiomycetes, Plasmodiophoromycetes, and Phycomycetes. These classes have been the subjects of previous chapters in this book.¹ Logical expansion of this concept ele-

¹ I have used Oömycetes, however, as a class name for Sparrow's Phycomycetes to designate the fungi whose motile cells possess one whiplash and one tinsel flagellum.

vates the old sub-class Zygomycetes to class rank and retains the old established name.

General Characteristics. The term Zygomycetes refers to the production of a sexual resting spore called a **zygospore** (Gr. *zygos* = yoke + *sporos* = seed, spore). A zygospore typically results from the complete fusion of two gametangia. It differs from an oöspore in that the latter is derived from an oösphere. The production of a zygospore is, therefore, the chief characteristic of members of this class. Nevertheless, a number of species in which no sexual reproduction has been found are classified in the Zygomycetes with complete confidence because they exhibit other characters which point to such relationships. Chief among these secondary characters is the production of characteristic sporangia or of conidia, and the complete absence of motile cells. Ecological, physiological, and biological considerations also enter into defining the Zygomycetes, which most mycologists consider as a natural group of fungi.

These are, then, the two main characteristics of the Zygomycetes: (1) sexual reproduction by means of gametangial copulation, resulting in the formation of a zygospore, and (2) asexual reproduction by means of non-motile spores in the form of sporangiospores or conidia.

Biologically, the Zygomycetes range all the way from saprobes, through facultative, weak parasites of plants, to specialized parasites of animals, and to obligate parasites of other Zygomycetes.

Certain groups of Zygomycetes are remarkably specialized in one way or another. Among the most interesting phenomena encountered in this class of fungi are (1) certain methods of spore dispersal, as exemplified by the "fungous shotgun" of *Pilobolus* and the repetitional germination and forceful propulsion of the "conidia" of the Entomophthorales, and (2) the animal-trapping mechanisms of the Zoöpagales.

Classification. The class Zygomycetes, as we recognize it here, includes three orders: Mucorales, Entomophthorales, and Zoöpagales. These may be distinguished in accordance with the following key:

SIMPLE KEY TO THE ORDERS OF THE CLASS ZYGOMYCETES

- A. Chiefly saprobic, some weakly parasitic on plants, a few endoparasitic in vertebrates, including man; asexual reproduction by sporangia containing one to many aplanospores, sometimes by conidia

Mucorales

AA. Chiefly parasitic on lower animals, rarely on plants, sometimes saprobic; asexual reproduction by modified sporangia functioning as conidia, or by true conidia

B. Modified sporangia functioning as conidia, forcibly discharged

Entomophthorales
Zoöpagales

BB. Conidia not forcibly discharged

order MUCORALES

Classification. The Mucorales have been investigated by a large number of workers on both sides of the Atlantic. In the previous century De Bary, Brefeld, Bainier, Coemans, Leger, Schroeter, Van Tieghem, and Vuillemin, among others in Europe, and primarily Thaxter in America laid down the morphological foundations of the classification of these fungi which produced the later monographs of Zycha (1935) and Naumov (1939). In later years, the cytological and physiological studies of Buller, Cutter, Sjöwall, Barnett and Lilly, and many others have extended our knowledge of the Mucorales along lines which had not been greatly explored in the past.

At the present time, the researches of Dr. C. W. Hesseltine of the U. S. Department of Agriculture, and of Dr. R. K. Benjamin of the Santa Ana Botanic Garden, are doing much to clarify the relationships among the Mucorales and to synthesize a modern system of classification from all the knowledge that has accumulated.

According to these workers (Hesseltine, 1952, 1955; Benjamin, 1959), the Mucorales have developed along six lines of evolution. The families which represent each line may be grouped as follows:

- | | |
|--------------------|-----------------------|
| 1. Mucoraceae | 5. Mortierellaceae |
| 2. Thamniaceae | Endogonaceae |
| Cunninghamellaceae | 6. Syncephalastraceae |
| 3. Choanephoraceae | Piptocephalidaceae |
| 4. Pilobolaceae | Dimargaritaceae |
| | Kickxellaceae |

In 1958 Boedijn added the family Helicocephalidaceae to accommodate the genera *Helicocephalum* and *Rhopalomyces*.

We can do little more in an introductory discussion than to point out some of the major characteristics of the order Mucorales with an occasional reference to special groups.

Biology. The great majority of the Mucorales are saprobes, living on such substrata as dung and decaying plant or animal matter. Many saprobic species are capable of synthesizing important indus-

trial products and have been utilized by man for his benefit. Thus, *Rhizopus stolonifer* (*R. nigricans*), the common bread mold, is used commercially for the manufacture of fumaric acid and for some steps in the manufacture of cortisone. *Rhizopus oryzae* is capable of producing considerable quantities of alcohol. Various species of *Rhizopus*, like *Rhizopus sinensis*, *Rhizopus stolonifer*, *Rhizopus oryzae*, and *Rhizopus nodosus*, are capable of forming large quantities of lactic acid. Although such lactic acid cannot compete in price with bacterial lactic acid, the mold product is of such great purity that it may find special usage (Foster, 1949). Mucorales also produce citric acid, succinic acid, oxalic acid, and other important chemicals. For a complete discussion of the biochemical activities of these and other fungi, see the excellent treatises entitled *Chemical Activities of Fungi*, by Dr. J. W. Foster of the University of Texas (1949), and *The Relation of Fungi to Human Affairs* by Dr. W. D. Gray of Ohio State University (1959).

A few Mucorales are weak parasites growing on fruits and other detached plant parts and causing diseases in transit and in storage. Such a one is *Rhizopus stolonifer*, which causes a serious transit disease of strawberries, designated as leak, and a soft rot of sweet potatoes in storage. Others are parasitic on fungi, green plants, or animals. *Choanephora cucurbitarum*, for example, attacks squash blossoms and fruits, sometimes causing considerable damage. Still other species of Mucorales are known to cause human diseases. *Absidia corymbifera* and several species of *Mucor* and *Rhizopus* attack the human internal nervous system with fatal consequences (Emmons, 1960/1961). Of particular interest to the mycologist are members of the family Piptocephalidaceae, which are obligately parasitic on other fungi, chiefly other Mucorales. These serve as ideal organisms for studies on the physiology of obligate parasitism. Such studies, now under way at West Virginia, are showing that temperature and nutrition greatly affect the susceptibility of the host to the parasite, and that nutrients provided the host often influence the growth of the parasite even when they do not affect the host itself (Berry and Barnett, 1957; Berry, 1959).

Somatic Structures. Typically, the soma of the Mucorales is a well-developed mycelium. In the few species in which the cytology of the somatic hyphae has been studied critically (Robinow, 1957; Bakerspigel, 1958) the nuclei appear to divide directly by constriction without spindle formation or evidence of classical mitotic figures. In most species the hyphae are coenocytic, producing septa at the bases of the reproductive organs, sporangia, or gametangia,

and only occasionally elsewhere when the mycelium ages. Such septa are solid plates formed by annular growth beginning at the hyphal wall. The more specialized Mucorales, in which the mycelium is septate from the very beginning, have perforate septa, some with tubular extensions projecting forward in the direction of protoplasmic flow, others with special type plugs (Benjamin, 1959). Protoplasmic streaming can easily be seen in vigorously growing hyphae of the Mucorales, and the mycelium of bread mold, so easy to isolate, is frequently used to demonstrate this phenomenon in the classroom.

The mycelium of some species produces rhizoids formed especially at points where the mycelium contacts a hard surface, such as the sides of a glass dish in which the fungus may be growing. The rhizoids adhere to the substratum and anchor the fungus securely. A hypha which connects two groups of rhizoids is called a stolon, and in function resembles the stolon of the strawberry, which grows out of the parent plant and strikes root at the tip. The similarity, of course, ends here.

Asexual Reproduction. The Sporangiphore. The Mucorales usually reproduce asexually by means of aplanospores contained in sporangia. They bear their sporangia on simple or branched sporangiophores. Branching varies from the relatively simple type of *Mucor*, through the whorled arrangement of *Thamnidium*, to the intricate differentiation of special coiled, fertile branches, which bear the **sporocladia** (sing. **sporocladium**; Gr. *sporos* = seed, spore + *klados* = branch) of *Spirodactylon* in the family Kickxellaceae.

The growth and development of the sporangiophores is a complicated process and has been studied extensively in *Phycomyces blakesleeanus*, which has become an extremely important tool for morphogenetic and physiological research. Particularly intriguing is the spiral growth of the sporangiophores, which appears to be correlated with a spiral arrangement of molecules in their walls (Castle, 1942, 1953).

The Sporangium. What we may regard as the typical sporangium of the Mucorales we find primarily in the Mucoraceae, the largest and probably the most primitive of the eleven families. Such a sporangium is formed at the tip of a sporangiophore as a globose swelling in which a central columella becomes separated from the outer sporiferous region. The typical sporangium, developed under favorable conditions, contains many thousands of spores.

In contrast to the above, some Mucorales produce small sporangia, with or without columellae, which contain but a few spores each,

and in some species are monosporous. We designate such small sporangia as *sporangiola* (sing. *sporangiolum*; *sporangium* + L. dimin. suffix *-olum*) or sporangioles (Figures 66B, C). Both sporangia and sporangiola may be, and frequently are, formed by the same sporangiophore in certain species. Sporangiola which contain but one spore are often regarded as conidia, and are so termed in the literature. This term applies particularly to structures in which the sporal and sporangial walls are completely fused and cannot be distinguished from each other (Figures 66D₁, E). Either term (*sporangiola* or *conidia*) may properly be applied to these structures, since it is probable that the conidia of the Zygomycetes have arisen from sporangia by reduction of the number of spores from many to one and by the subsequent fusion of the wall of the sporangium with that of the single spore within it.

Figure 66 shows at a glance some of the structures which suggest to mycologists that the conidium of the Mucorales has been developed from the sporangium. Look at the drawing (A) of the large sporangium of *Blakeslea trispora*. This may be regarded as a typical sporangium of the Mucorales. Now study the sporangiola arising from a central head (B). These represent reduced sporangia arising from a branched sporangiophore. Branched sporangiophores are common in the Mucorales. Next in line (C, C₁) are the three-spored sporangiola on small heads at the branched tip of the sporangiophore. The next probable step toward the development of the conidium takes us to the genus *Choanephora* (D, D₁). The inflated heads (D) now support sporangiola which contain but a single spore or in which the spore wall appears to be fused with the sporangial wall (D₁). Once this stage is reached, you can see how *Cunninghamella* (E), which produces conidia on inflated conidiophores, may have developed.¹

The fungi included in the most advanced evolutionary series of the Mucorales produce their spores in cylindrical sporangiola which we call *merosporangia* (sing. *merosporangium*; Gr. *meros* = portion + *sporangium*). Merosporangia may be borne on the surface of an inflated sporangiophore tip and radiate out, or they may be formed on sporocladia. In the Syncephalastraceae the merosporangia contain many uniseriate spores; in the Piptocephalidaceae from

¹ This discussion is not meant to imply that the genera mentioned as examples of different sporangial types have evolved one from the other, or even that they are related. Sporangia and conidia have apparently arisen several times in the various developmental lines along which the Mucorales appear to have evolved.

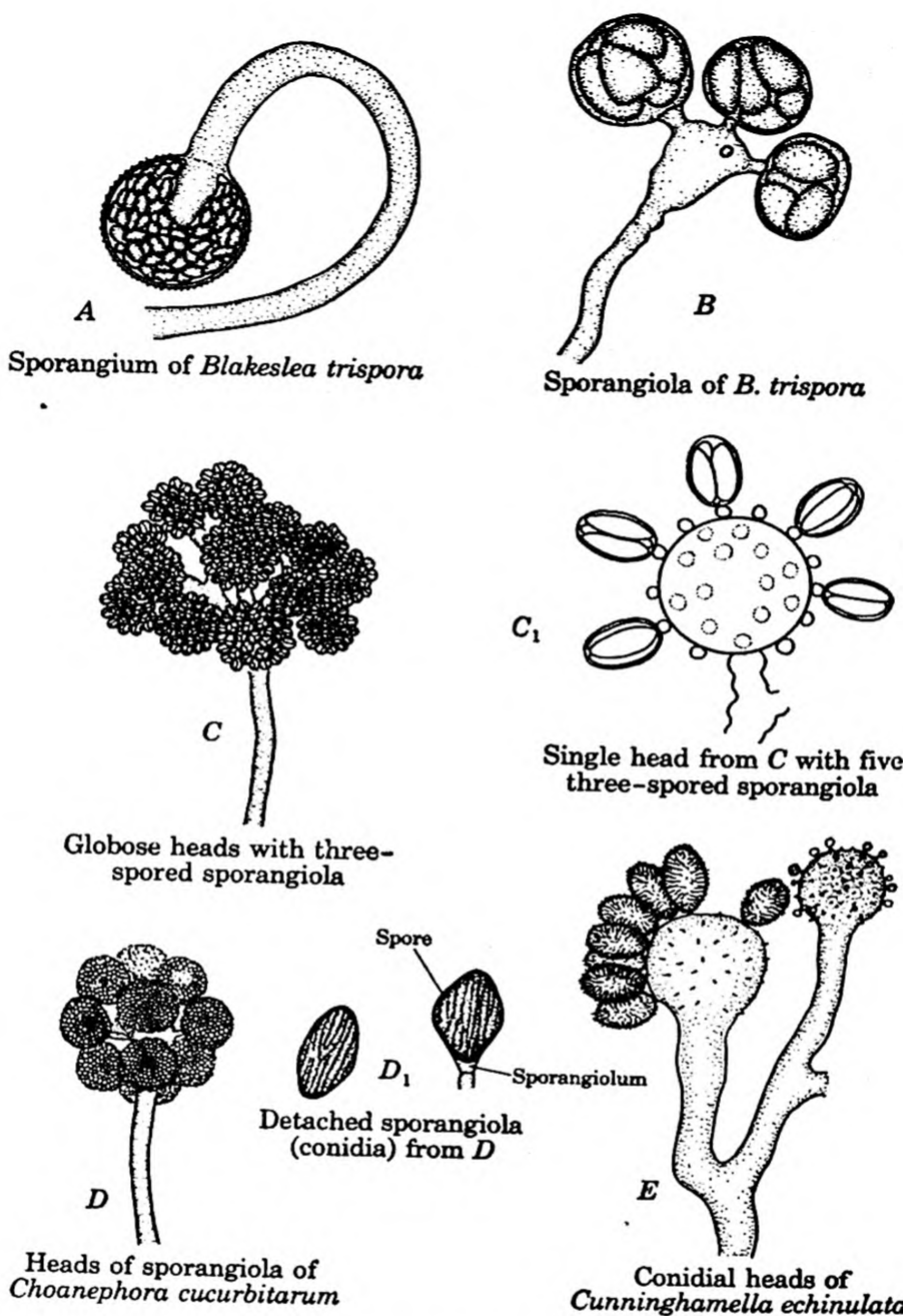


Figure 66. Series of drawings showing probable transition stages in the evolution of the sporangium to a conidium. A–C, D₁, redrawn from Thaxter, 1914, *Bot. Gaz.*, 58:353–366; E, redrawn from Thaxter, 1891, *Bot. Gaz.*, 16:14–26; all by permission of University of Chicago Press, Chicago; D, redrawn from Thaxter, 1903, *Rhodora*, 5:97–102.

one to many spores; and the Dimargaritaceae, two spores. The Kickxellaceae bear monosporous sporangiola on special cells produced on sporocladia (Figure 67).

Spores and Spore Dissemination. Sporangiospores differ in shape, size, markings, and color. In the majority of species they are globose to ovoid; in some species they are cylindrical. In many forms the spores are longitudinally striate. Some bear long hyaline bristles at each pole. Sporangiospores are usually formed by the cleavage of the sporangial protoplast into minute uninucleate or multinucleate portions around each of which a wall develops. If the spores are uninucleate at the time of their formation, they often become multinucleate later by nuclear division. Special methods of spore formation are employed by some members of the more advanced families.

The sporangiospores are liberated by the dissolution of the sporangial wall. In some Mucorales the spores form a dry, powdery mass and are easily dispersed by air currents, but in other species the spore mass is enveloped by a drop of liquid which dries and leaves the spores adhering firmly to each other and to the columella.

Of great interest is the mechanism of spore dispersal developed by *Pilobolus*, a common inhabitant of horse and cow dung. The entire sporangium is violently shot off the sporangiophore and adheres to the first solid object it strikes. The sporangiophores of *Pilobolus* are positively phototropic and shoot their sporangia toward the light. This is a useful adaptation which helps disseminate the spores.

The sporangiophore of *Pilobolus* consists of a swollen trophocyst (Gr. *trophe* = food + *kystis* = bladder), the sporangiophore proper, a swollen sub-sporangial vesicle, and a sporangium whose wall is heavily cutinized (Figure 68). Buller (1934) states that *Pilobolus* can shoot its sporangia vertically upward to a height of 6 feet. Thus *Pilobolus* (the hat thrower) deserves its name.

Other methods of asexual reproduction in the Mucorales include the formation of chlamydospores—sometimes referred to as gemmae—in the hyphae, and the breaking up of the mycelium into yeast-like bodies which reproduce by budding. Yeast-like cells are formed when the mycelium is growing in a liquid medium.

Physiology of Asexual Reproduction. Exactly what triggers the initiation of asexual reproduction in the Mucorales is not known, but considerable progress has been made in the study of conditions which favor or inhibit the formation of asexual reproductive structures. Of particular interest are the researches of Barnett and Lilly (1950, 1955) at West Virginia with *Choanephora cucurbitarum*, an organ-

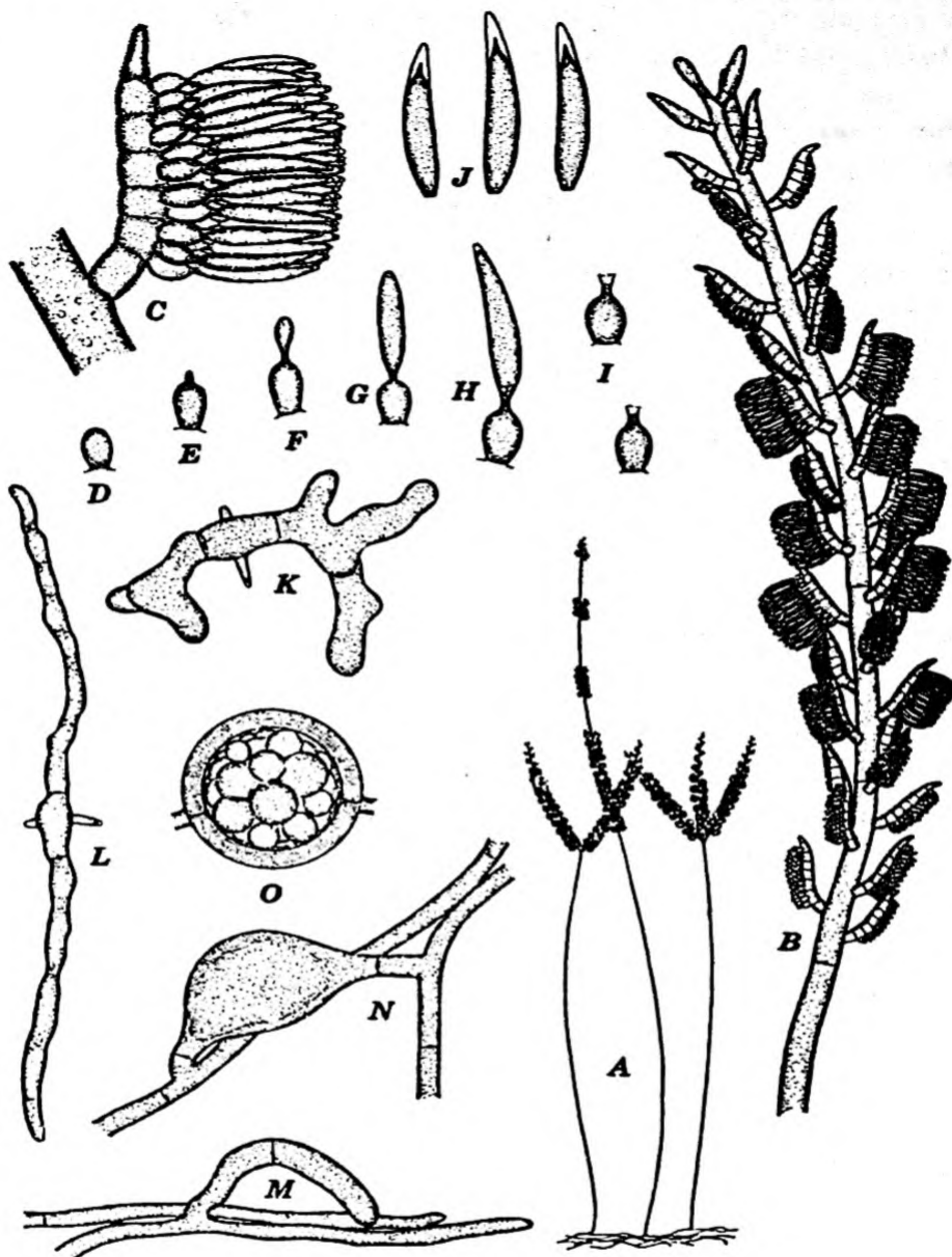


Figure 67. *Coemansia mojavensis*. A. Habit sketch. B. Upper portion of fruiting branch. C. Sporocladium. D-H. Stages in the development of a sporangiolum. I. Collar-like remnant of the basal portion of the sporangiolum wall. J. Mature sporangiola. K-L. Germinating spores. M. Plasmogamy. N. Early stage of zygospore. O. Mature zygospore. Courtesy R. K. Benjamin, 1958, *El Aliso*, 4:149-169.

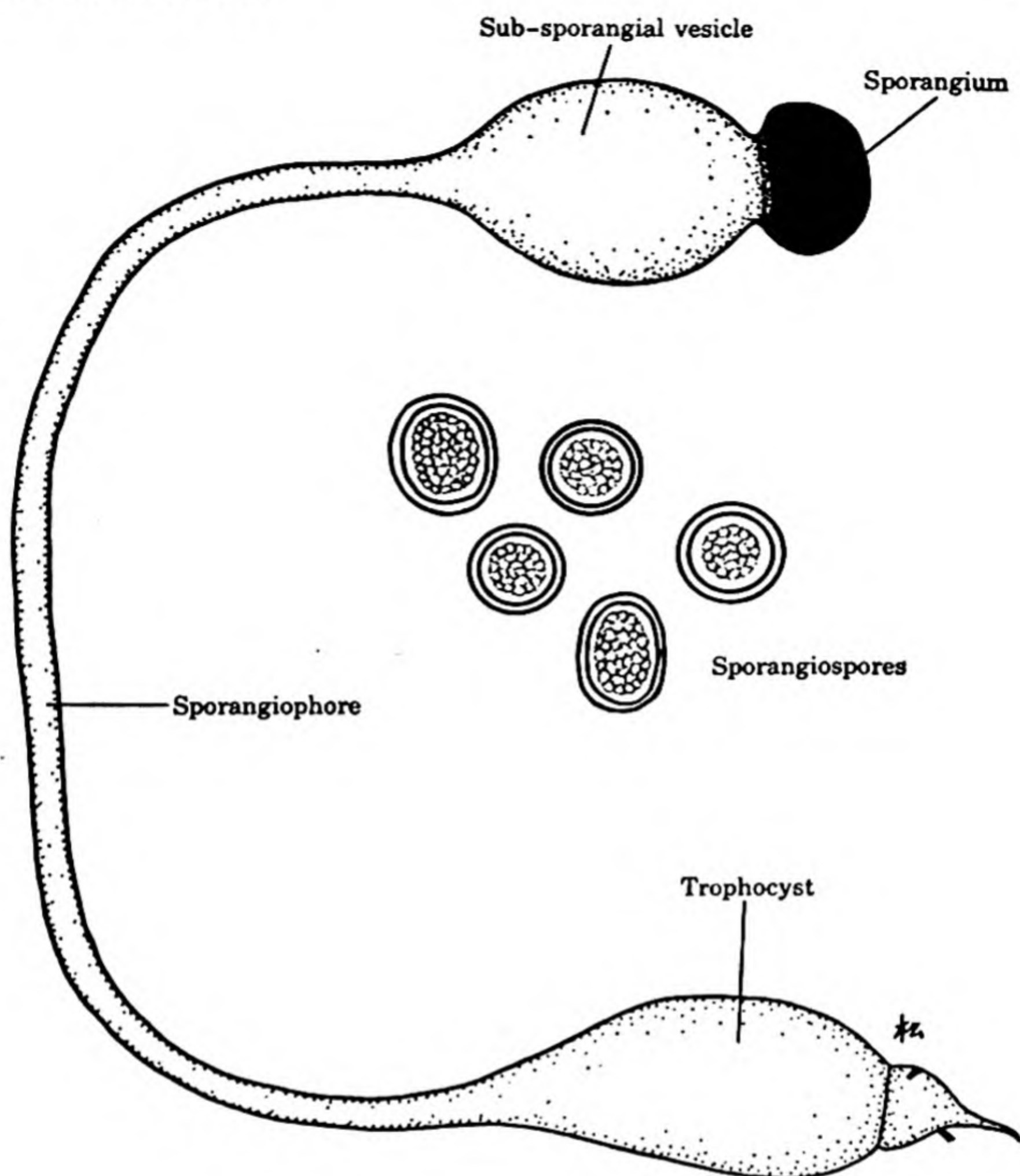


Figure 68. *Pilobolus longipes*. Sporangial apparatus.

ism which produces both multispored sporangia and monospore sporangiola (conidia). High temperature ($30-31^{\circ}\text{C.}$) and relative humidity (100 per cent) favor sporangial production and inhibit formation of conidia. Lower temperature (25°C.) and relative humidity favor conidial production. The effect of light is even more spectacular. No conidia are produced in continuous darkness, continuous bright light (60 foot-candles), or darkness followed by bright light. However, when a period of bright light *precedes* a period of darkness, abundant conidia are formed. Some conidia are

also formed in continuous weak light (less than 1 foot-candle). The possible explanation proposed is that some substance necessary for the formation of conidia is synthesized in two steps, the first of which requires light and the second of which is inhibited by light (Figure 69).

We have already mentioned the genus *Pilobolus* in connection with its spore dispersal mechanism. Until recently, we could grow *Pilobolus* in the laboratory only on media containing dung decoctions. Hesseltine and his coworkers (1952) found in dung a factor which was necessary for the growth of *Pilobolus*. They named this factor coprogen. That same year Page (1952) announced that he had grown *Pilobolus* on a chemically defined medium with hemin as a substitute for the necessary growth factor in dung. However, even though *Pilobolus* grew well in such a medium, production of sporangia was meager. Continuing with this work, Page noticed that

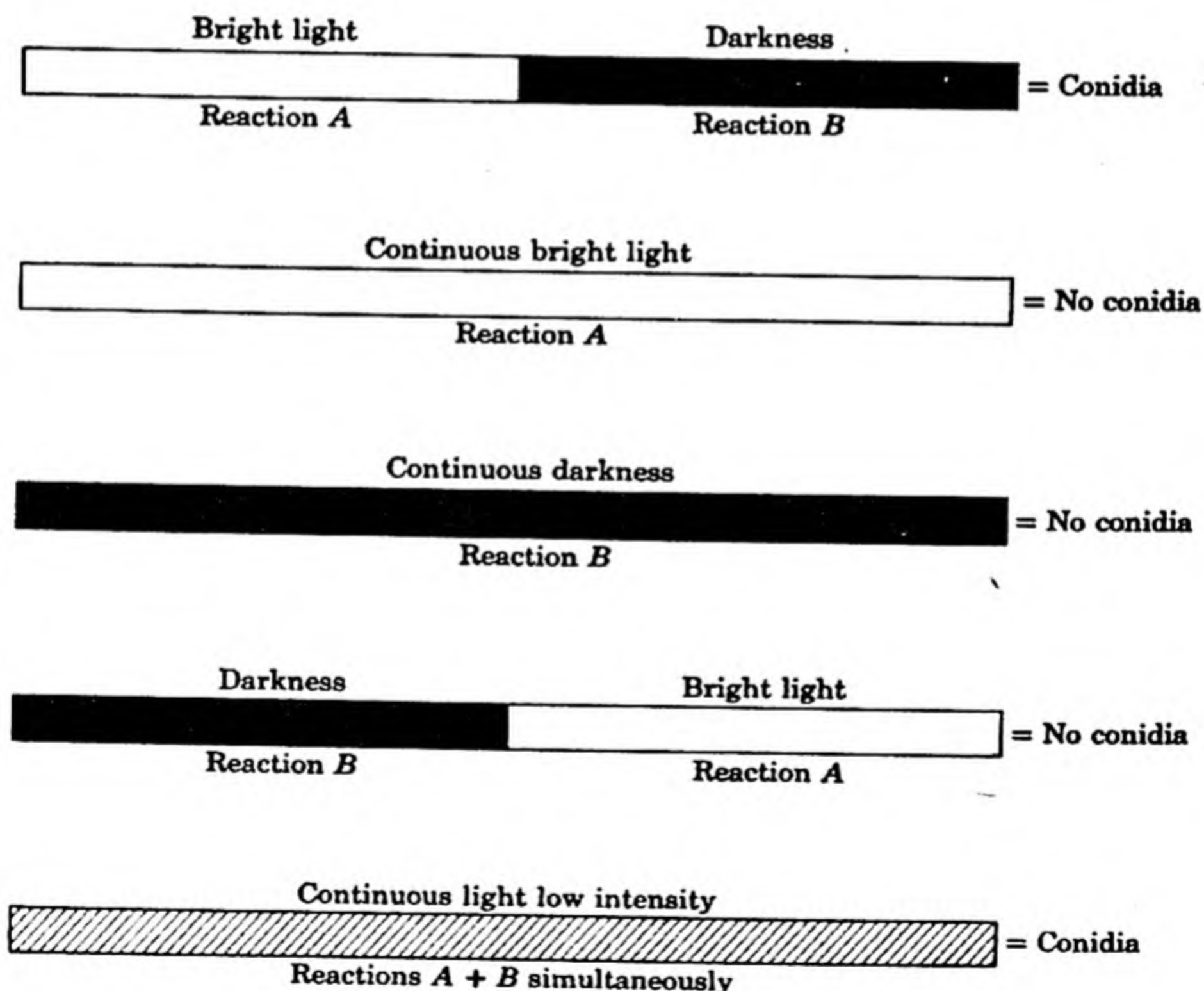


Figure 69. *Choanephora cucurbitarum*. Conidium formation under different light conditions. Courtesy Barnett and Lilly, 1955, *Phytopath.*, 40:80-89.

some plates contaminated with *Mucor plumbeus* produced much larger numbers of sporangia than pure cultures of *Pilobolus*. Further work showed that the stimulatory substance is ammonia and that the fungus uses the ammonium ion in preference to other N sources investigated (Page, 1959, 1960/1961).

Sexual Reproduction. Sexual reproduction in the Mucorales takes place by the copulation of two multinucleate gametangia which are in the main similar in structure, but which may differ in size. The gametangia are produced as terminal swellings on the tips of two compatible hyphae or hyphal branches which are attracted one to the other and come in contact. When the gametangia are formed, the walls between them dissolve and the contents mix. The cells of the two gametangia thus actually fuse into one cell, in which karyogamy eventually takes place. This cell develops into a zygospore by the deposition of a thick wall around its protoplast. We shall discuss the details of sexual reproduction and zygospore formation in the next section of this chapter.

It was in the Mucorales that Dr. A. F. Blakeslee, the great American geneticist, discovered in 1904 the phenomenon of sexual incompatibility in fungi. Species which could produce zygospores on single thalli Blakeslee called homothallic; species which required two compatible thalli to form zygospores he called heterothallic. Since the two compatible strains could not be distinguished morphologically, Blakeslee labeled one + and the other -.

Twenty years after Blakeslee's discovery of heterothallism, Burgeff (1924), in a series of experiments, demonstrated that a diffusible substance is probably responsible for the initiation of sexual reproduction in the Mucorales. This was the first demonstration of a hormonal sexual mechanism in the fungi. Burgeff, working with a number of species, showed that, when + and - strains were separated by a collodion membrane, hyphae of opposite strains were still attracted toward each other. Subsequent work by other investigators (Banbury, 1954, 1955; Plempel, 1957, 1960; Plempel and Braunitzer, 1958) has expanded upon Burgeff's discovery, and is giving us some knowledge as to the nature of the hormones involved and their method of operation.

As might be expected, sexual reproduction in the Mucorales is influenced by environmental factors, but few studies have been undertaken to determine optimum conditions for zygospore development. Barnett and Lilly (1956) have shown that in *Choanephora cucurbitarum* zygospores form under a much greater range of conditions than asexual spores. Light has little effect on zygospore formation,

by germ tube (Figures 70D, D') which develops into a fluffy, many-branched, white, aerial mycelium (Figures 70A, A'). The mycelium produces many aerial stolons which develop rhizoids at certain points. Directly above the rhizoids, one or more sporangio-phores are produced (Figures 70B, B'). The top of each sporangio-phore becomes swollen as the latter reaches maturity, and a sporangium begins to develop. During its development a great deal of cytoplasm carrying many nuclei flows into the young sporangium and concentrates mainly in its periphery.

The central portion of the sporangium becomes highly vacuolated and is eventually surrounded by a wall which separates it from the peripheral zone. This central portion is the columella, and the peripheral zone is the spore-bearing portion of the sporangium. The protoplasm of the peripheral zone soon becomes divided into a large number of multinucleate segments, which eventually round off, become enveloped by walls, and mature into sporangiospores. With the bursting of the sporangial wall and the liberation of the spores, which fill the air, the asexual cycle of *Rhizopus stolonifer* is completed. Other Mucorales follow the same general pattern, but the structures produced may differ in detail. Thus the majority of the Mucorales do not form stolons or rhizoids; some have no columella differentiated in the sporangium; some have branched sporangio-phores; and in some the sporangia may be replaced or accompanied by sporangiola.

Sexual reproduction in *Rhizopus stolonifer* requires the presence of two physiologically distinct and compatible mycelia, + and -, the fungus being heterothallic. All structures which have originated as a result of the germination of a single sporangiospore are of the same strain as the parent spore. When two opposite strains come in contact with one another, copulating branches called **progametangia** (sing. **progametangium**; Gr. *pro* = before + *gametangium*) are formed (Figure 70E). Much cytoplasm and many nuclei flow to the contacting tips of these organs, which now begin to enlarge. A septum then forms near the tip of each progametangium, separating it into two cells: a terminal gametangium and a suspensor cell (Figure 70F). The walls of the two contacting gametangia dissolve at the point of contact, and the two protoplasts mix (Figure 70G). The nuclei pair, one + with one -, and the two nuclei in each of a number of pairs fuse and form diploid nuclei. Unfused nuclei probably disintegrate (Cutter, 1942b). In the meantime the new cell which has been formed by the copulating gametangia enlarges considerably, its wall thickens, and its surface becomes black and

warty. This heavily walled structure is the zygosporangium (Figure 70H). At 21° C. under laboratory conditions, the zygosporangia of *Rhizopus stolonifer* germinate in approximately 1–3 months (Gauger, 1961), apparently requiring a rest period before they are activated. At the time of germination the zygosporangium cracks open and a sporangiophore emerges and develops a sporangium, called a germ sporangium, at its top. Meiosis takes place during the process of zygosporangium germination.

Zygosporangium formation in other Mucorales takes place essentially in the same manner as described for *Rhizopus stolonifer* but differs in detail. Many Mucorales are homothallic, and consequently each thallus is self-fertile. The size and shape of the gametangia may differ considerably. Thus, in *Phycomyces* the gametangial apparatus resembles calipers holding a zygosporangium between their tips. The suspensors in this genus are provided with black, horn-like projections which give the zygosporangium apparatus a characteristic appearance (Figure 71A). In *Zygorhynchus*, another genus of Mucorales, the gametangia as well as the suspensors are unequal in size (Figure 71B). Members of this genus are homothallic. The size and outer sculpturing of the zygosporangia also differ in different genera. It is particularly interesting to note that in the genus *Mortierella* the zygosporangium is surrounded by a large number of short hyphae which form a cottony envelope around it (Figure 71C). In the genus *Endogone* this tendency is carried further, and a number of closely associated zygosporangia are enclosed within a hyphal peridium, thus forming a fruiting body. Such species are believed by some mycologists to represent the ancestral line from which the Ascomycetes have developed.

Both homothallic and heterothallic species may and do occur in the same genus of the Mucorales. In the segregation of strains during meiosis, the Mucorales seem to fall into several groups. The first of these includes the homothallic species in which all sporangiospores in the germ sporangium give rise to homothallic mycelia. In the second group, typified by *Mucor mucedo* and certain other heterothallic species, all the spores in a germ sporangium are of the same mating type, + or -. In a third group of Mucorales, also composed of heterothallic species, typified by *Phycomyces nitens*, each germ sporangium contains at least three kinds of spores: +, -, and \pm . Finally, *Rhizopus stolonifer*, in accordance with the results obtained by Gauger (1961), is unique among the Mucorales which have been studied in that its germ sporangia contain either one type of sporangiospore (+ or -) or two types of spores: + and -.

Inasmuch as meiosis takes place before the spores of the germ sporangium are formed, we would logically expect all Mucorales to conform to this last pattern of mating type segregation, with half the sporangiospores of the germ sporangium containing $+$ nuclei and the other half $-$ nuclei.

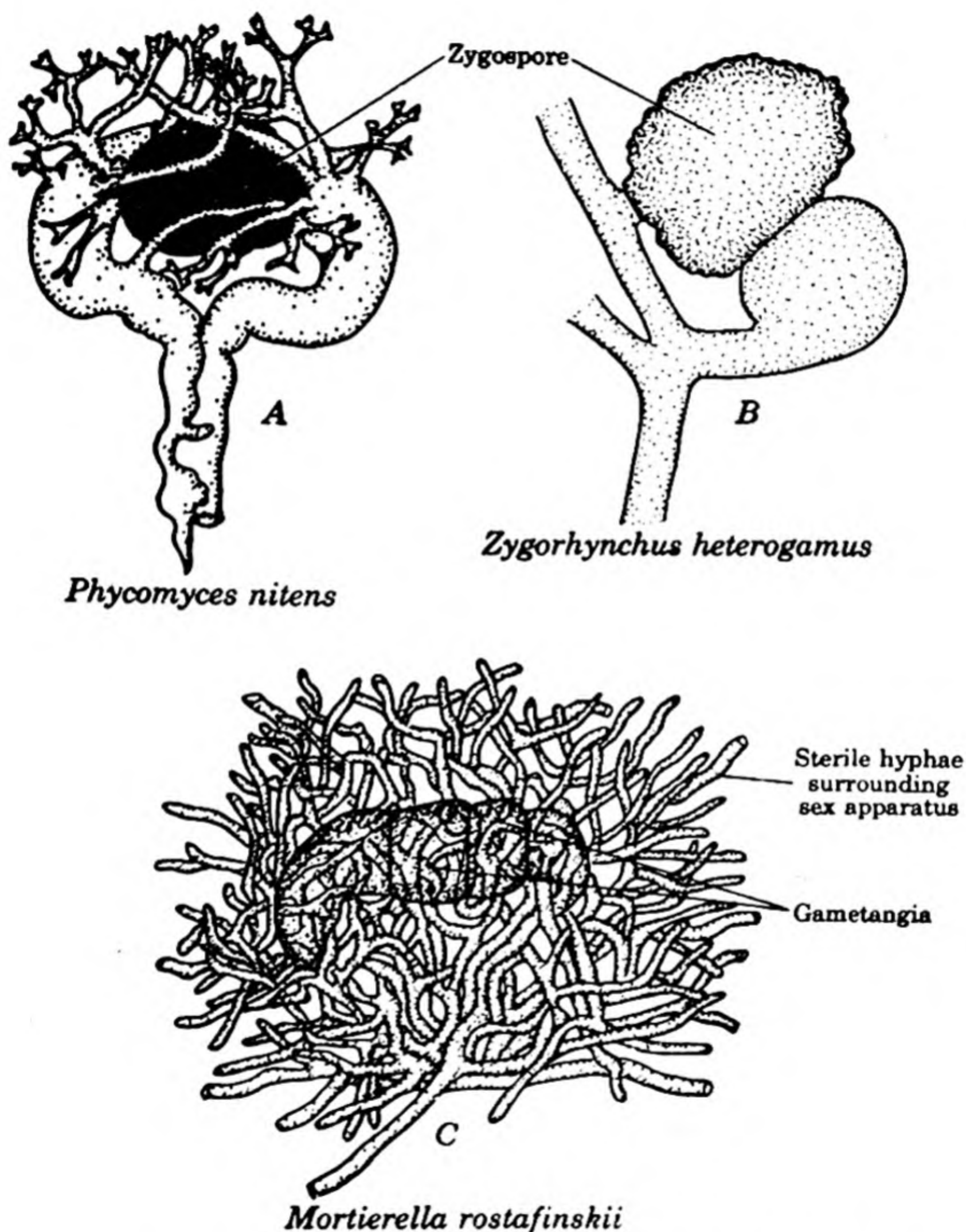


Figure 71. Zygosporangia of Mucorales. A, redrawn from van Tieghem and Le Monnier, 1873, *Ann. sci. nat. Bot.*, 5 ser., 17:261–399; B, redrawn from Blakeslee, 1913, *Mycol. Centralbl.*, 2:241–244; C, redrawn from Brefeld, in Rabenhort's *Kryptogamen Flora*, 1892, Vol. I, E. Kummer, Leipzig.

Cutter (1942*a, b*) and Sjöwall (1945, 1946) have attempted to give us the cytological explanation for the different segregation patterns. In the homothallic forms, such as *Sporodinia grandis* (Figure 72), there is, of course, no problem. It is interesting, however, to note that, according to Cutter, no nuclear fusion takes place in this species, so that no diploid nuclei are formed. Cutter's conclusions contradict those of earlier investigators on this point. In *Mucor mucedo*, in which only one mating type survives in the germ sporangium, all the gamete nuclei fuse in pairs resulting in many diploid nuclei, and meiosis occurs before the resting period sets in. All but one of the nuclei resulting from meiosis apparently disintegrate. The surviving nucleus multiplies by division, and its progeny enter the germ sporangium and become incorporated in the spores. Whether the surviving nucleus is of the + or - mating type is probably a matter of chance.

In *Rhizopus stolonifer* many nuclei fuse in pairs, but some remain unfused. However, the unfused nuclei degenerate and the diploid

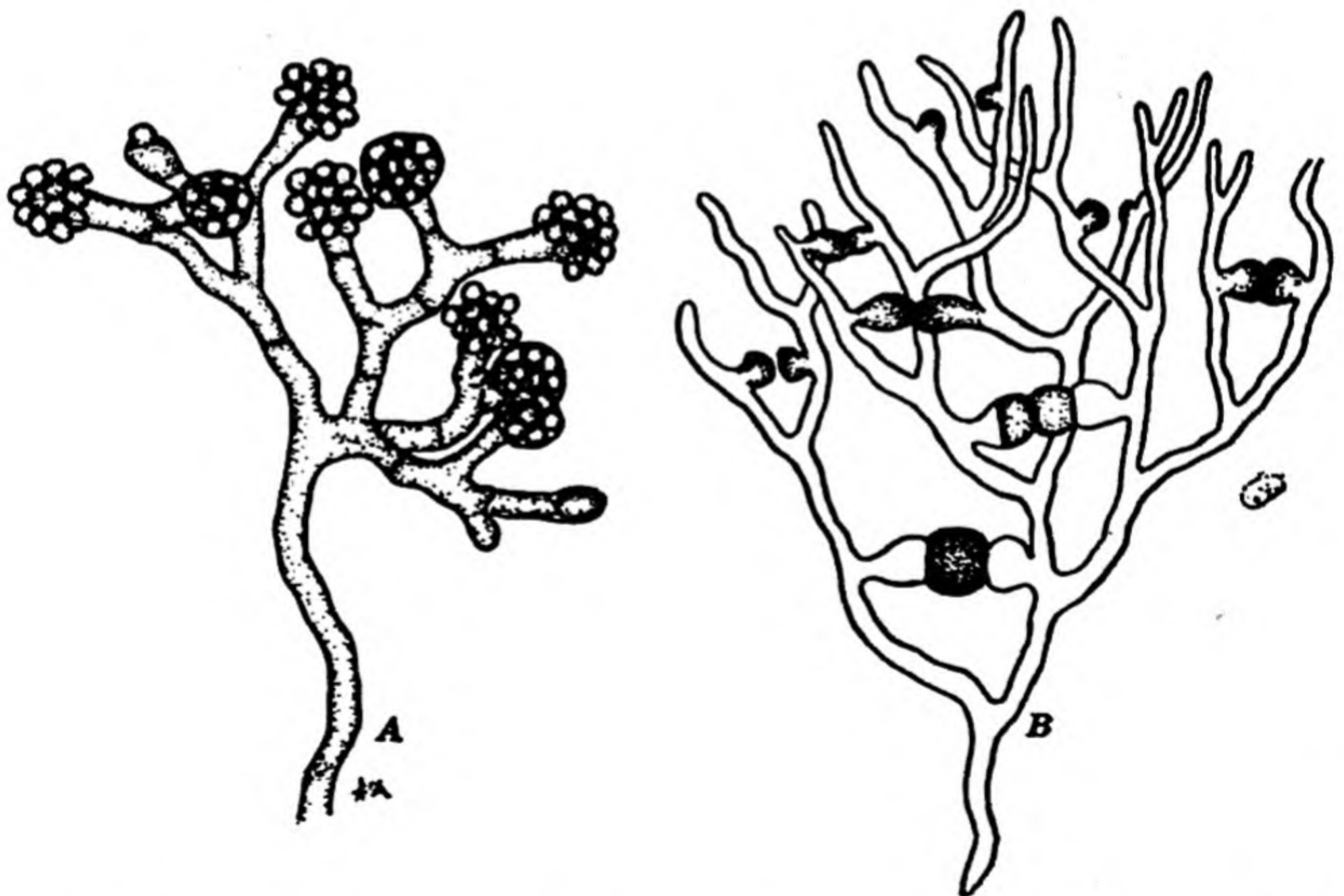


Figure 72. *Sporodinia grandis*. A. Sporangiophore. B. Zygomphore. B, redrawn from Bonarden, in Rabenhorst's *Kryptogamen Flora*, 1892, Vol. I, E. Kummer, Leipzig.

nuclei undergo meiosis after the rest period, just before germination (Cutter, 1942b). Half the haploid nuclei resulting from meiosis are of the $+$ and half of the $-$ mating type. Germ sporangia which contain both spore types receive both $+$ and $-$ nuclei. In *Phycomyces blakesleeanus* both karyogamy and meiosis are delayed until germination occurs. Some nuclei fuse at this time and some remain unfused. Some of the diploid nuclei then undergo meiosis, but others do not. This condition results in a mixture of haploid $+$, haploid $-$, and diploid \pm nuclei. When these become incorporated in the spores, the germ sporangium obviously contains at least three kinds of spores. The diploid spores give rise to homothallic mycelia; or, if the nuclei are reduced, either in the spore or in the hyphae during division, the spores may give rise to heterokaryotic mycelia which behave as homothallic. The proportion of \pm nuclei diminishes with each asexual generation until no more \pm spores are formed.

order ENTOMOPHTHORALES

The Entomophthorales include fungi which are chiefly parasitic on insects. *Basidiobolus ranarum* is the cause of a serious human disease (Emmons *et al.*, 1957). A few species are parasitic on the lower forms of plants, and several are saprobic on animal matter such as the excreta of frogs or lizards. The most familiar of the Entomophthorales is *Entomophthora muscae*, commonly called the fly fungus, which is often found on the dead bodies of houseflies clinging to long-unwashed windowpanes in attics, garages, and . . . university classrooms. If you examine such a fly on a windowpane, you will find a wide, white, halo-like zone on the glass, surrounding the dead fly. This white zone consists of innumerable conidia which have been shot off the conidiophores growing out of the body of the fly. This forcible ejection of the conidia is a prominent characteristic of the Entomophthorales. Two families are recognized: Entomophthoraceae and Basidiobolaceae.¹

Somatic Structures. The mycelium of the Entomophthorales is not so extensive as that of the Mucorales as a rule. In the Entomophthoraceae the mycelium has a definite tendency to form septa and then to fragment into portions which we call **hyphal bodies**. Such bodies multiply by division or budding, and each eventually produces a

¹ Ciferri *et al.* (1956) also include the family Paracoccidioidaceae in the Entomophthorales. This includes three genera of fungi parasitic in man and animals. No sexual stage has been found in any species included here.

conidiophore bearing a conidium at its tip. In some species, such as *Entomophthora fumosa* and *Entomophthora fresenii*, hyphal bodies copulate and develop zygosporangia. Some of the saprobic species have a well-developed mycelium which persists as such. The mycelium of the Basidiobolaceae is also septate and persistent. It consists of uninucleate cells.

Few of the Entomophthorales have been grown in culture. The saprobic species, such as *Conidiobolus brefeldianus*, grow rather easily on artificial media. A few of the entomogenous species have been grown on special media rich in animal proteins. Wolf (1951) grew *Entomophthora apiculata* and *Entomophthora coronata* on a chemically defined medium with ammonium or amino N. He found that nitrate N cannot be utilized, that only a few sugars (glucose, levulose, galactose, mannose, trehalose) can serve as a C source for these fungi, and that no external supply of vitamins is required.

Asexual Reproduction. The Entomophthorales reproduce asexually by means of sporangiola, functioning as conidia, which are borne on simple or branched conidiophores. The conidia are forcibly discharged from the conidiophores, and, in most species, germinate by producing germ tubes. However, in the genus *Basidiobolus*, a common inhabitant of the excreta of frogs and lizards, the "conidium" becomes a sporangium at the time of germination, for it produces a number of aplanospores by the segmentation of its protoplast. In some species of *Entomophthora* too, Thaxter (1888) showed that the conidium is in reality a one-spored sporangium in which the spore can be seen after the "conidium" has remained in water for some time. These examples constitute important evidence of the evolution of the conidium from a sporangium in the Entomophthorales.

The conidia of the Entomophthorales are covered by a mucilaginous substance which adheres to any object against which the conidium is catapulted. In *Entomophthora muscae* (Figure 73) and other species, if the conidium lands on a substratum suitable for its growth, it germinates and forms mycelium; otherwise it produces a secondary conidium. This process may be repeated until either a substratum suitable for growth is reached, or the protoplasm is exhausted in the third or fourth conidial generation.

Sexual Reproduction. Zygosporangia are formed in several species, but their further development is unknown. It is probable that they germinate by means of germ tubes. In principle, zygosporangium formation in most Entomophthorales investigated is similar to that in the Mucorales, but the details are somewhat different and characteristic

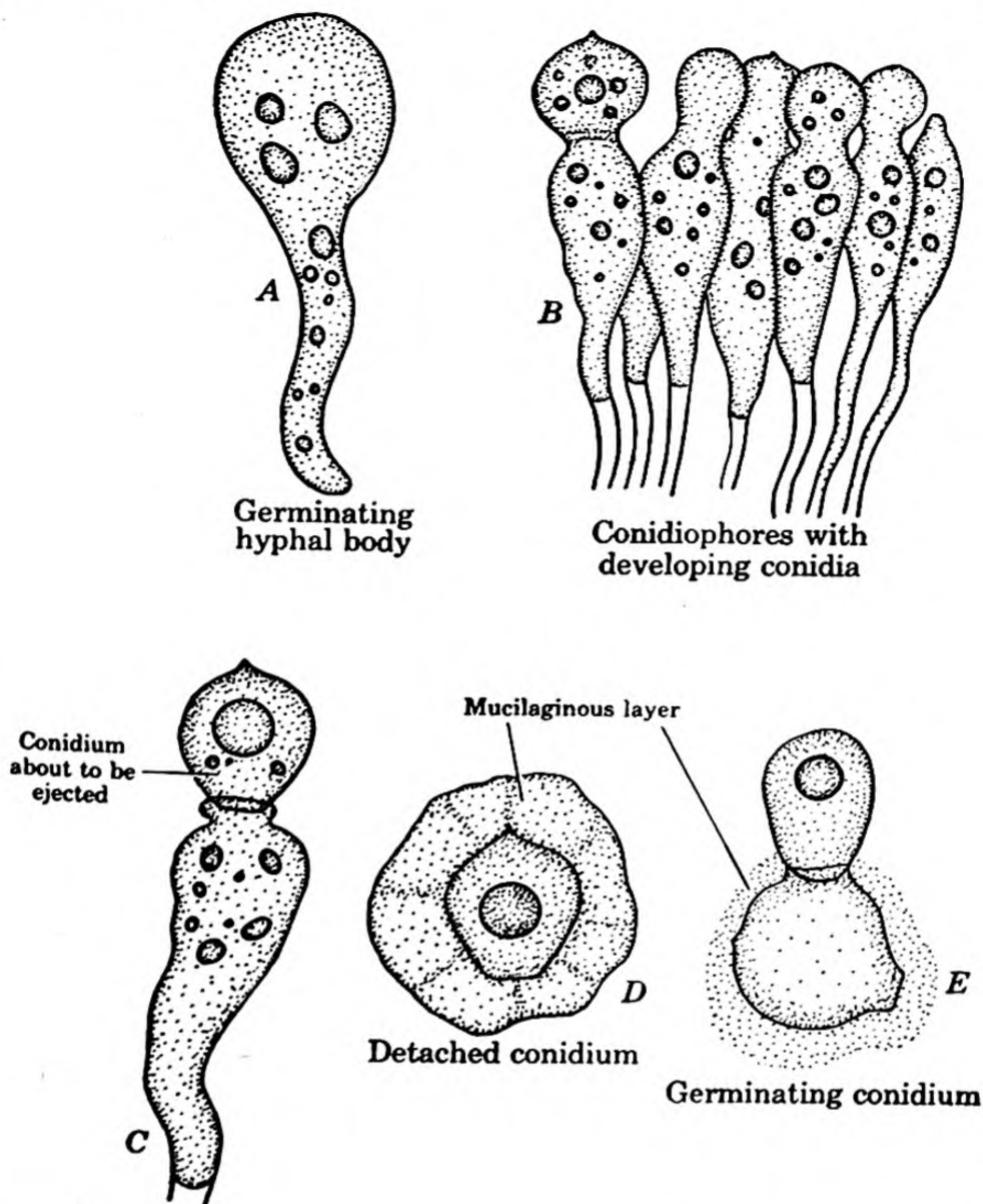


Figure 73. *Entomophthora muscae*. Redrawn from Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.*, 4:133-201.

of the group. The copulating gametangia may be mycelial cells, as in the Mucorales, or hyphal bodies (Figure 74). The zygospore may be formed by the enlargement of one of the two copulating gametangia or from an outgrowth arising between the two fusing cells or from one of them after fusion. In the genus *Conidiobolus*, zygospore formation differs radically from that in other genera. Here, two un-

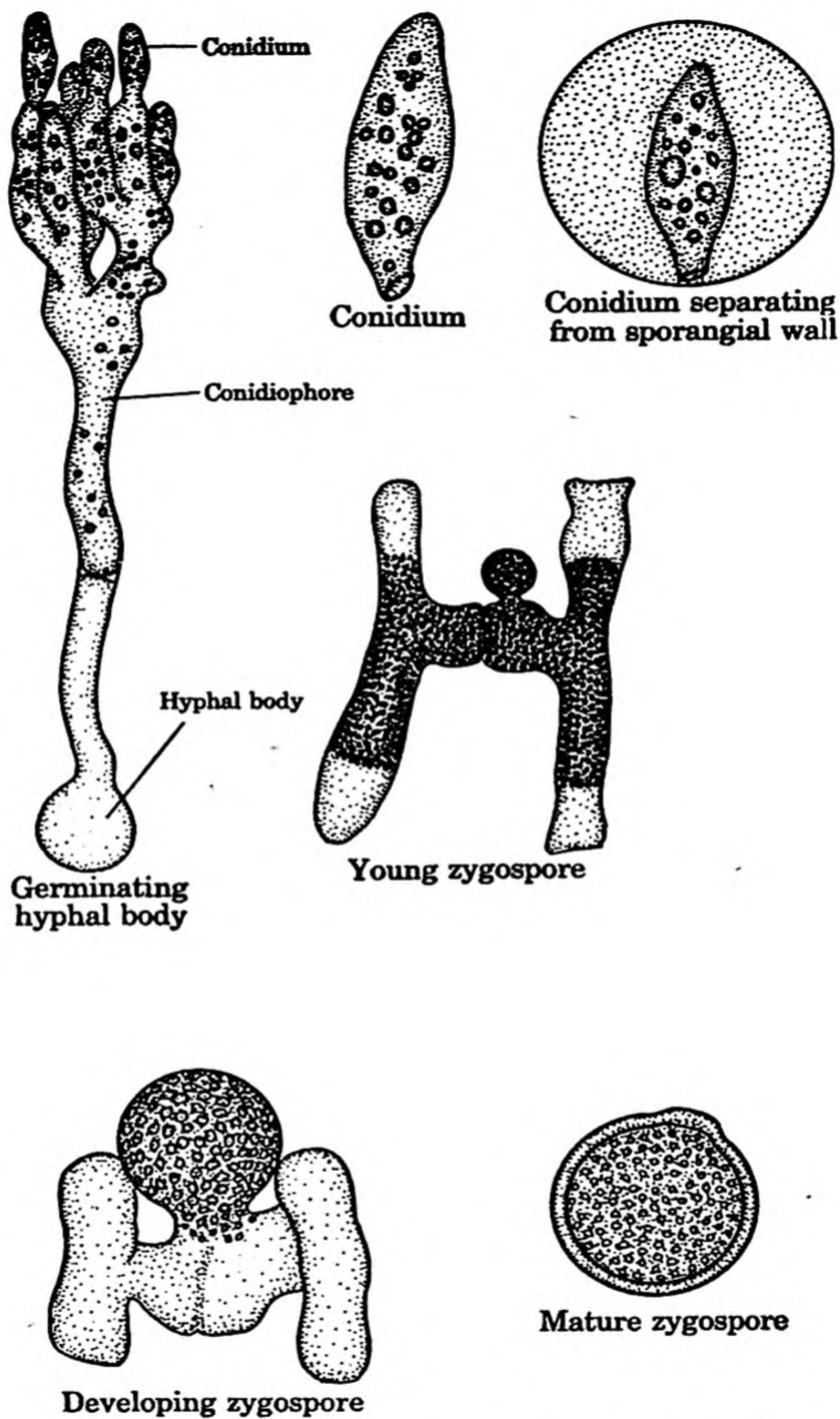


Figure 74. *Entomophthora sepulchralis*. Redrawn from Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.*, 4:133–201.

equal gametangia come in contact and the contents of the smaller one pass into the larger one through a pore. The resting spore then develops within the larger gametangium. This is somewhat reminiscent of sexual reproduction in the Oömycetes, but no oösphere, periplasm, or fertilization tube ever develops, so that, in spite of the irregularity in its formation, the resting spore is considered a zygospor.

In certain species (*Entomophthora muscae*) zygosporae are formed parthenogenetically without gametangial fusion. Such structures are known as azygosporae (Gr. *a* = not + *zygos* = yoke + *sporos* = spore). In structure they are similar to zygosporae and presumably carry on the function of resting spores as well as true zygosporae do.

order ZOÖPAGALES

Introduction. Our knowledge of the Zoöpagales we owe entirely to the researches of Dr. Charles Drechsler of the U. S. Department of Agriculture, who discovered these organisms. In 1935 Drechsler proposed that they be recognized as a distinct family and suggested that they may be worthy of ordinal rank. In 1938 he published a formal description of the family Zoöpagaceae. Bessey treated these organisms as an order in 1950, and we are adopting this view here. Some mycologists (Martin, 1961), however, consider them closely enough related to the Entomophthorales to include the Zoöpagaceae in that order.

The order Zoöpagales consists of the single family Zoöpagaceae with about ten genera, such as *Endocochlus*, *Cochlonema* (Figure 75), *Bdellospora*, *Zoöpage*, *Stylopage*, *Euryancale*, and *Cystopage*. For descriptions and illustrations see Drechsler's papers in *Mycologia*, only a few of which are listed in the References at the end of this chapter.

General Characteristics. The Zoöpagales are especially adapted for parasitizing small animals such as amoebae, rhizopods, and nematodes. They reproduce asexually by true conidia which are not forcibly discharged, and sexually by the formation of zygosporae. Their gross morphology and general life history have been worked out by Drechsler (1935, etc.), but their cytology and physiology still remain unknown.

Somatic Structures. Three forms of thalli are recognized. In the predaceous species the soma consists of an aseptate, extensive mycelium which branches irregularly and gives rise to variously branched haustoria within the captured animals, which are para-

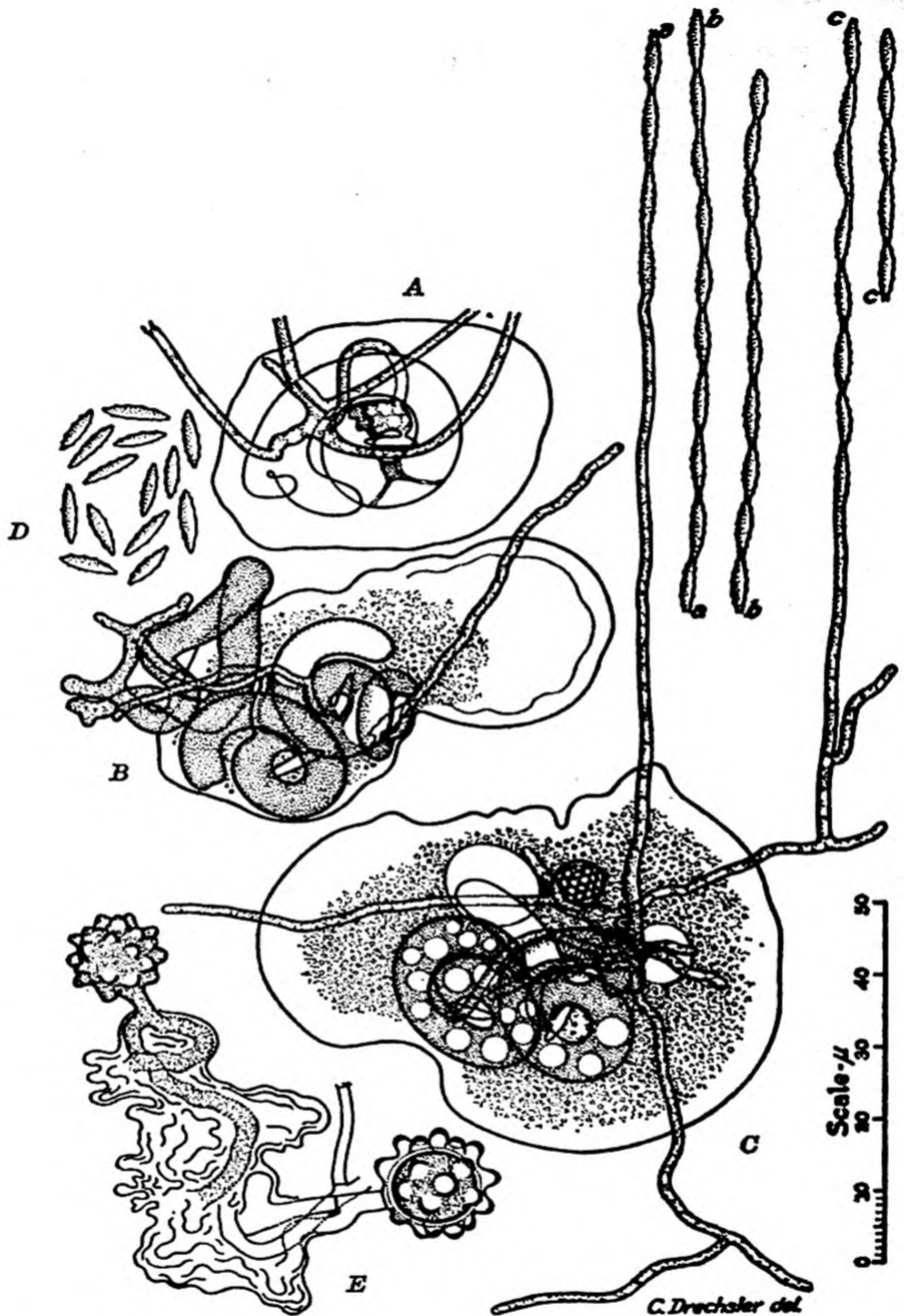


Figure 75. *Cochlonema verrucosum*. A. Amoeba enveloping a single thallus of the parasitic fungus. B. Dying amoeba with three internal thalli of the parasite. C. Conidial chains shown in sections, whereof a, b, and c represent corresponding points. D. Mature conidia. E. Zygosporangia, one containing a nearly mature zygospore. Courtesy Drechsler, 1935, *Mycologia*, 27:6–39.

sitized. In the endoparasitic species the soma consists of a short thick hypha which may be spirally wound, forming a coil within the parasitized animal. In ectoparasitic species a swollen conidium, adhering to the host externally, germinates and produces a haustorium which branches inside the host.

Asexual Reproduction. In some forms (*Cystopage*) asexual reproduction is solely by means of chlamydospores. Most species, however, produce aerial, thread-like, spindle-shaped, or globose conidia. These are borne singly, in chains, or in loose heads at the tips or sides of conidia-bearing hyphae or conidiophores. The conidia break off the hyphae which bear them and germinate, either on the surface of a susceptible host to which they adhere, or inside it if they are ingested.

Sexual Reproduction. Sexual reproduction occurs by the union of two hyphal tips acting as gametangia. These usually originate from separate spores, possibly indicating that the fungi are heterothallic. A zygosporangium enclosed in a wall (zygosporangium) is thus formed. Germination of the zygosporangium has not been seen, nor, as stated before, has the nuclear cycle been worked out.

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10 class TRICHOMYCETES

Neither the limits nor the taxonomic position of this group of organisms is as yet clear.

The chief character which binds them together is, perhaps, their association with the arthropods. As defined by Martin (1961), the Trichomycetes are fungi with a simple or branched filamentous thallus attached by a basal cell to the digestive tract or the external cuticle of living arthropods. The mycelium is limited in extent and is not immersed in the tissues of the host.

The class Trichomycetes as treated here is probably a heterogeneous group including organisms which may not be related. Miss Manier (1955a) of the zoölogical laboratory at Montpellier, France, divides the group Trichomycetes into two classes, three orders, and ten families. Martin (1961) accepts Lichtwardt's (1960/1961) classification and considers the Trichomycetes to be a sub-class (Trichomycetidae) of the class Phycomycetes, consisting of five orders. We shall discuss only one of these, the Eccrinales, and that very briefly.

order ECCRINALES¹

The Eccrinales are fungi which live inside the bodies of arthropods, usually attached to the intestinal tract of the animal. They do not appear to be parasites but are rather commensals. They are probably widely distributed, having been reported from Europe, North and South America, Africa, and some parts of southeast Asia. As more biologists become interested in their study they will undoubtedly be found in all parts of the world.

Somatic Structures. The soma of the Eccrinales is limited in extent. It consists of a long, slender, unbranched, straight or spirally

¹ This discussion is based chiefly on papers by Dr. R. W. Lichtwardt of the University of Kansas.

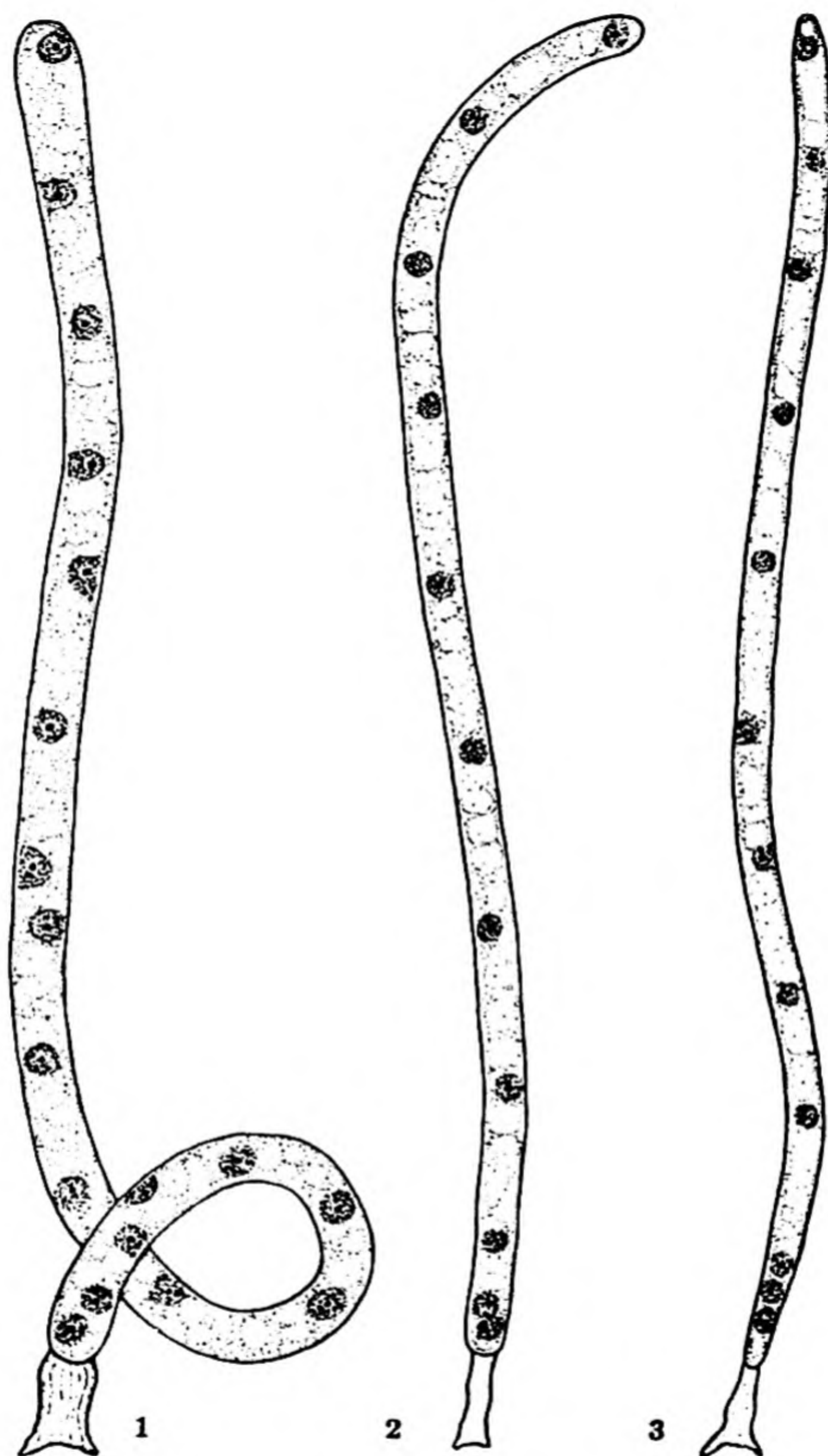


Figure 76. Thalli of three species of Eccrinales, showing coenocytic hyphae and holdfasts. Courtesy Lichtwardt, 1954, *Mycologia*, 46:564-585.

curved, coenocytic hypha with walls that contain cellulose. The basal part of the hypha is in the form of a disc-like holdfast by means of which the fungus is attached to the host (Figure 76).

Asexual Reproduction. The Eccrinales reproduce asexually by means of spores variously formed in the hyphal tips. Lichtwardt (1954, 1958) recognized nine types, two of which are common.

1. Multinucleate Sporangiospores (Figure 77A). These spores are formed singly in linearly arranged sporangia separated by cross-walls. The mature spores are multinucleate (four to eight), and each is discharged through a hole in the sporangial wall. They can germinate within the gut of the host that produced them, thus serving as a means of building up the number of thalli endogenously.

2. Uninucleate Sporangiospores (Figure 77B). Similar in their formation to the multinucleate spores, these are shorter and remain uninucleate. Some produce a heavy wall. These spores pass through the digestive tract and serve to infect other susceptible individuals that ingest them.

Sexual Reproduction. Whether sexual reproduction occurs in the Eccrinales is still a matter of conjecture. Fusion of protoplasts has been reported in some species, resulting in the formation of zygotes which become converted into resting spores.

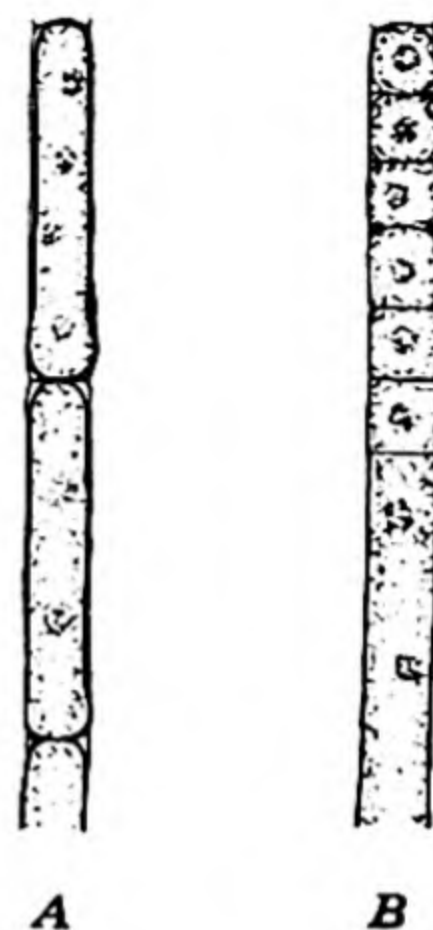


Figure 77. *Enterobryus borariae*. Multinucleate (A), and uninucleate (B) spores within a hyphal tip. Courtesy Lichtwardt, 1958, *Mycologia*, 50:550-561.

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PART IV THE HIGHER FUNGI

11 class ASCOMYCETES the sac fungi

Introduction. The Ascomycetes and the Basidiomycetes are sometimes called higher fungi. They are considerably more advanced than the fungi we have studied up to now, as shown by their complexity of structure, and are possibly derived from the lower fungi, although some mycologists believe they have had an independent origin (Bessey, 1942, 1950; Dodge, 1914). The yeasts, some of the common black molds and green molds, the powdery mildews, the cup fungi, the morels, and the truffles are among the best-known examples of Ascomycetes.

Occurrence, and Importance to Man. Ascomycetes can be found in a variety of habitats and at most seasons of the year. Many are small and inconspicuous, parasitic on plants, and evident only from the effects they produce upon their hosts. Others are saprobic, live on the soil or on decaying logs and leaf mold, and produce large, easily discernible fruiting bodies. A few are entirely *hypogean* (Gr. *hypo* = under + *ge* = earth), developing and remaining underground. A number of Ascomycetes are *coprophilous* (Gr. *kopros* = dung + *philein* = to love), growing only on the dung of certain animals.

The plant parasitic Ascomycetes, many of which develop their spores in the dead leaves of their hosts, you may best collect in early spring when their spores are mature and about to be released. Others, such as the saprobic cup fungi, you can find in the woods throughout the growing season. For some species, such as the morels, the fruiting season is short, not exceeding 3 or 4 weeks.

The marine Ascomycetes, which were formerly neglected by mycologists, are now being studied in a number of marine laboratories (Johnson and Meyers, 1957; Johnson and Sparrow, 1961; Wilson,

1960). Marine Ascomycetes may be saprobic on various types of organic material submerged or floating in marine waters or may be parasitic on marine algae and higher plants.

The Ascomycetes are of great importance in human affairs. The cellulolytic Ascomycetes, such as *Chaetomium* (Figure 111), are among the organisms responsible for the destruction of fabrics containing cellulose. In destroying crops and crop plants as well as timber and ornamental trees, the Ascomycetes are among our worst fungous enemies, causing such diseases as apple scab, brown rot of stone fruits, powdery mildews, foot rot of cereals, ear rot of corn, and many others. The chestnut blight, caused by the ascomycete *Endothia parasitica*, has completely annihilated the chestnut forests of America, and the Dutch elm disease, caused by another ascomycete, *Ceratocystis ulmi*, threatens the American elm with extinction. Some diseases of our domestic animals and of man himself are of ascomycetous origin; aspergillosis, a respiratory disease, is one example; body ringworm, another. Of interest in this connection is the ergot fungus, *Claviceps purpurea*, an ascomycete whose mycelium invades and destroys the ovaries of the rye plant, thus causing a plant disease, and in so doing produces sclerotia with alkaloids which are deadly to animals and human beings if consumed. (See page 322 for the life history of this fungus.)

On the other hand, many Ascomycetes are beneficial. The fermenting activities of certain yeasts are the basis of the baking and brewing industries; food yeast played a significant role in the nutrition of the German people during World Wars I and II and may become more and more important as a diet supplement the world over when population pressures create greater problems of food supply than exist at present. The morels and truffles enjoy a fame of special importance among the fungi, for discriminating eaters consider them second to none in delicacy of flavor.

If we include in the Ascomycetes those imperfect fungi (Deuteromycetes) which probably have ascomycetous affinities, the Ascomycetes become of tremendous importance indeed. We shall discuss the Deuteromycetes in Chapter 18.

General Characteristics. The one character which distinguishes the Ascomycetes from all other fungi is the ascus, a sac-like structure containing a usually definite number of ascospores (Gr. *askos* = goat skin, sac + *sporos* = seed, spore) formed as a result of karyogamy and meiosis. Eight ascospores are typically formed within the ascus, but this number may vary from one to over a thousand according to the species. Other characteristics of the Asco-

mycetes are a septate mycelium, the production by most species of a fruiting body enclosing the asci, and the complete absence of any type of flagellated cell. These, however, are secondary characteristics which occur in other fungi as well. If a fungus produces its spores in asci, it is an ascomycete regardless of any other character; if it does not, it may not be properly placed in this class.

The Ascomycetes in general have two distinct reproductive phases, the ascus or sexual stage, often called the **ascigerous** or **perfect stage**, and the conidial or asexual stage, often designated as the **imperfect stage**. There are, however, a number of Ascomycetes whose conidial stages, if they exist, have not been found. Since ascomycete classification is based entirely on the characteristics of the perfect stage, such forms do not present a problem to the systematist. On the other hand, a very large number of fungi exist which are known only by their conidial stages. Since these imperfect stages are similar to those of known Ascomycetes, it is almost certain that many of the so-called imperfect fungi (*Fungi Imperfecti*) are actually Ascomycetes which have either lost their ascus stages as a result of their evolutionary development, or which possess ascus stages as yet undiscovered. In either case, this large group of imperfect Ascomycetes constitutes one of the greatest taxonomic problems of the mycologist. Because of their great importance to man, a separate chapter (18) under the heading of Deuteromycetes is devoted to them.

Somatic Structures. The mycelium of the Ascomycetes is composed of septate hyphae the walls of which contain a large proportion of chitin. The hyphae are well developed, slender or stout, and profusely branched. The formation of septa begins at the hyphal periphery and advances toward the center, leaving a minute hole in the middle (Figure 78). This hole permits protoplasmic strands to pass from one cell into the next, thus establishing organic connection between all parts of the mycelium. The cells of the mycelium are often uninucleate, but mycelia consisting of multinucleate cells are also quite common.

If the mycelium of an ascomycete originates from the germination of a single, uninucleate spore, the mycelium will be homokaryotic. Heterokaryotic mycelium may originate in a variety of ways (see page 28). Of importance in this connection are the perforations in the hyphal septa which permit nuclei to migrate from one compartment (cell) of a hypha to another. Thus, if a single compartment of a homokaryotic mycelium becomes heterokaryotic, either through mutation in one of its nuclei or through the introduction of new,

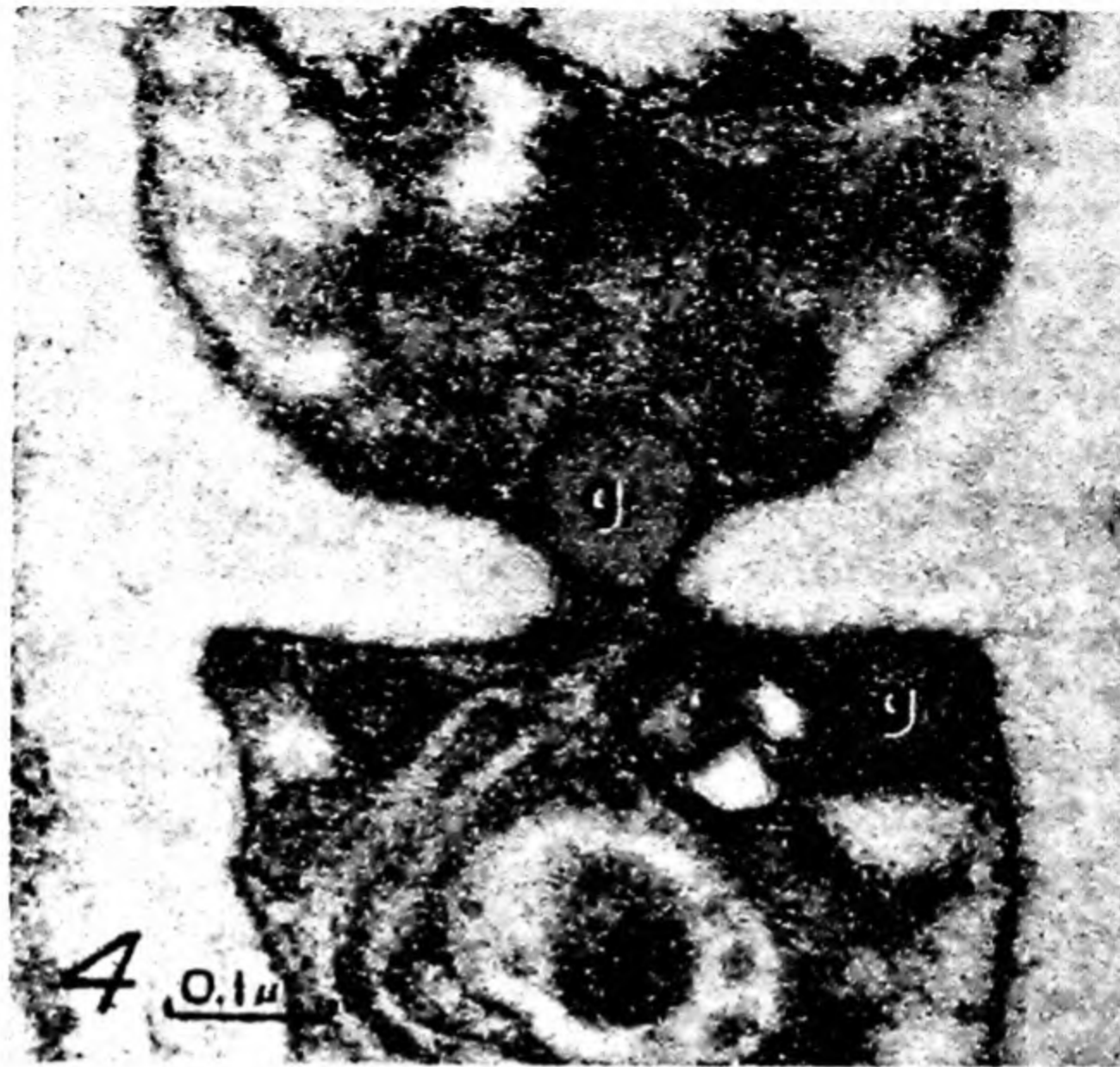


Figure 78. Electron micrograph of septum in a hypha of the ascomycete *Neobulgaria pura*, showing simple pore. Courtesy Moore and McAlear, 1962, *Am. Jr. Bot.*, 49:86–94.

genotypically different nuclei, the entire mycelium will soon become heterokaryotic by the multiplication, migration, and spread of the new nuclei among the original nuclear population. Such migration has been observed in living mycelium, and moving pictures have been taken of nuclei passing through septa. Dr. Keeping (E. S. Dowding, 1958) of the University of Alberta, who has made a study of nuclear migration in *Gelasinospora* (page 310), reports that nuclei in *Gelasinospora tetrasperma* are carried by the streaming cytoplasm at speeds which reach 40 mm. per hour.

Ascomycete mycelium is often organized into fungal tissues. If such a tissue is loosely woven and the mycelial strands are more or less evident, it is known as prosenchyma (Figure 7A). If, however, the tissue is closely woven, if the hyphae have lost their individuality, if the cells are more or less isodiametric, and if the tissue in general resembles the parenchyma of plants, it is known as pseudoparenchyma (Figure 7B).

Prosenchymatous and pseudoparenchymatous tissues are chiefly associated with the spore-bearing (fruiting) bodies of Ascomycetes.

But certain somatic structures, such as sclerotia and stromata, are also composed of these tissues, especially of pseudoparenchyma, as mentioned in Chapter 1.

Not all Ascomycetes possess mycelium. As we shall see in the next chapter, some yeasts are unicellular; others produce a chain of cells which form a false mycelium (pseudomycelium); still others are unicellular under certain conditions, but mycelial under others.

Asexual Reproduction. Asexual reproduction in the Ascomycetes may be carried on by fission, budding, fragmentation, arthrospores, chlamydospores, or conidia, according to the species and to the environmental conditions.

Fission and budding are methods of propagation normally encountered in the yeasts (Figure 11) and in a few other Ascomycetes. Spores produced by budding are called blastospores (Gr. *blastos* = a bud + *sporos* = spore).

Since all living portions of the thallus are potentially capable of growth, fragmentation, whether natural or artificial, under favorable conditions results in as many new individuals as there are fragments.

Conidia are formed by a great many—perhaps the majority of—Ascomycetes. It is in fact in this class of fungi that conidial development has reached its zenith as indicated by the great variety of conidial forms produced. As in the lower fungi, here too the asexual stages carry the burden of propagating and disseminating the species throughout the spring and summer, several generations of conidia being produced during the growing season.

Conidia are generally produced on conidiophores. These vary from extremely short, nearly obsolete hyphae to those that are long and intricately branched (Figure 79). Conidiophores may be produced free from each other, without any evident organization, arising from ordinary somatic hyphae, or they may be organized into definite fruiting bodies. The most common of such fruiting bodies are: (1) the **pycnidium** (pl. **pycnidia**; Gr. *pyknos* = concentrated + *-idion*, dimin. suffix), which is a hollow, generally globose or flask-shaped structure whose pseudoparenchymatous walls are lined with conidiophores (Figure 80A), and (2) the **acervulus** (pl. **acervuli**; L. *acervus* = heap, dimin. form), a mat of hyphae usually formed, by parasitic fungi, below the epidermis or cuticle of the plant host and giving rise to short conidiophores closely packed together, forming a bed-like mass (Figure 80B). Conidiophores may also be cemented together to form complex structures such as sporodochia and syn-

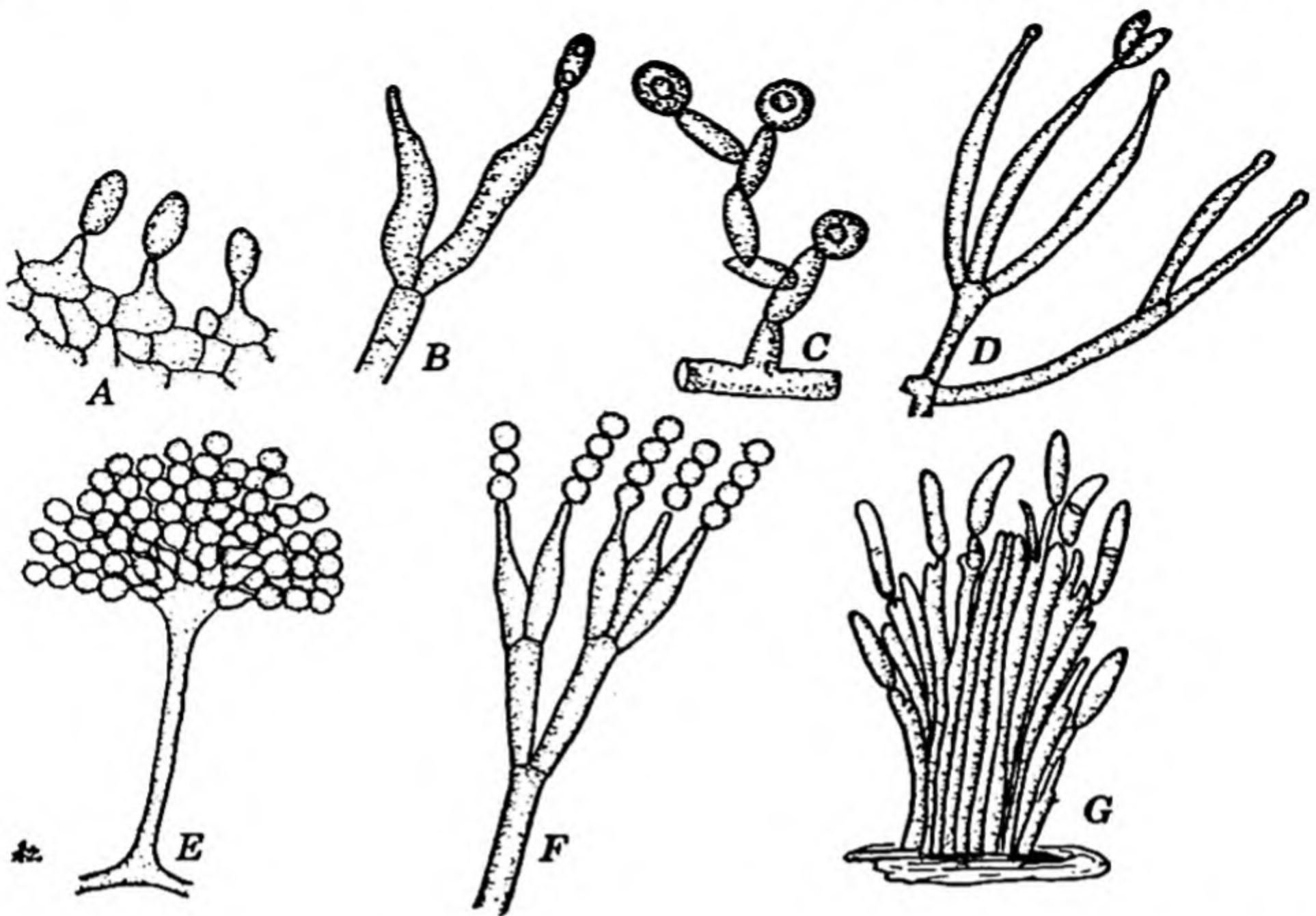


Figure 79. Various types of conidiophores bearing conidia. A. *Phyllosticta*. B. *Dendrophoma*. C. *Monopodium*. D. *Verticillium*. E. *Aspergillus*. F. *Penicillium*. G. *Isariopsis*. C, redrawn from Delacroix; G, redrawn from Boudier; both in Engler and Prantl, 1900, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^{oo}, Wilhelm Engelmann, Leipzig.

nemata (Figures 80C, D), which will be described in the discussion of the Deuteromycetes in Chapter 18.¹

Sexual Reproduction. Sexual reproduction in the Ascomycetes, as in other living organisms, aims at the union of two compatible nuclei. These nuclei are brought together in the same cell by one of the many methods developed by the Ascomycetes during their evolution. We have seen that in a great many of the lower fungi such nuclei fuse soon after they are brought together. In the Ascomycetes such is not the case. Here, the two nuclei remain in close association and undergo successive divisions which usually result in a number of dikaryotic cells.

Nuclear fusion eventually takes place in the ascus mother cell,

¹ It is essential that you understand the relation between conidial and ascus stages before you proceed much further in the study of the Ascomycetes. I urge you strongly, therefore, to read pages 387–401 in Chapter 18 as soon as you finish this chapter.

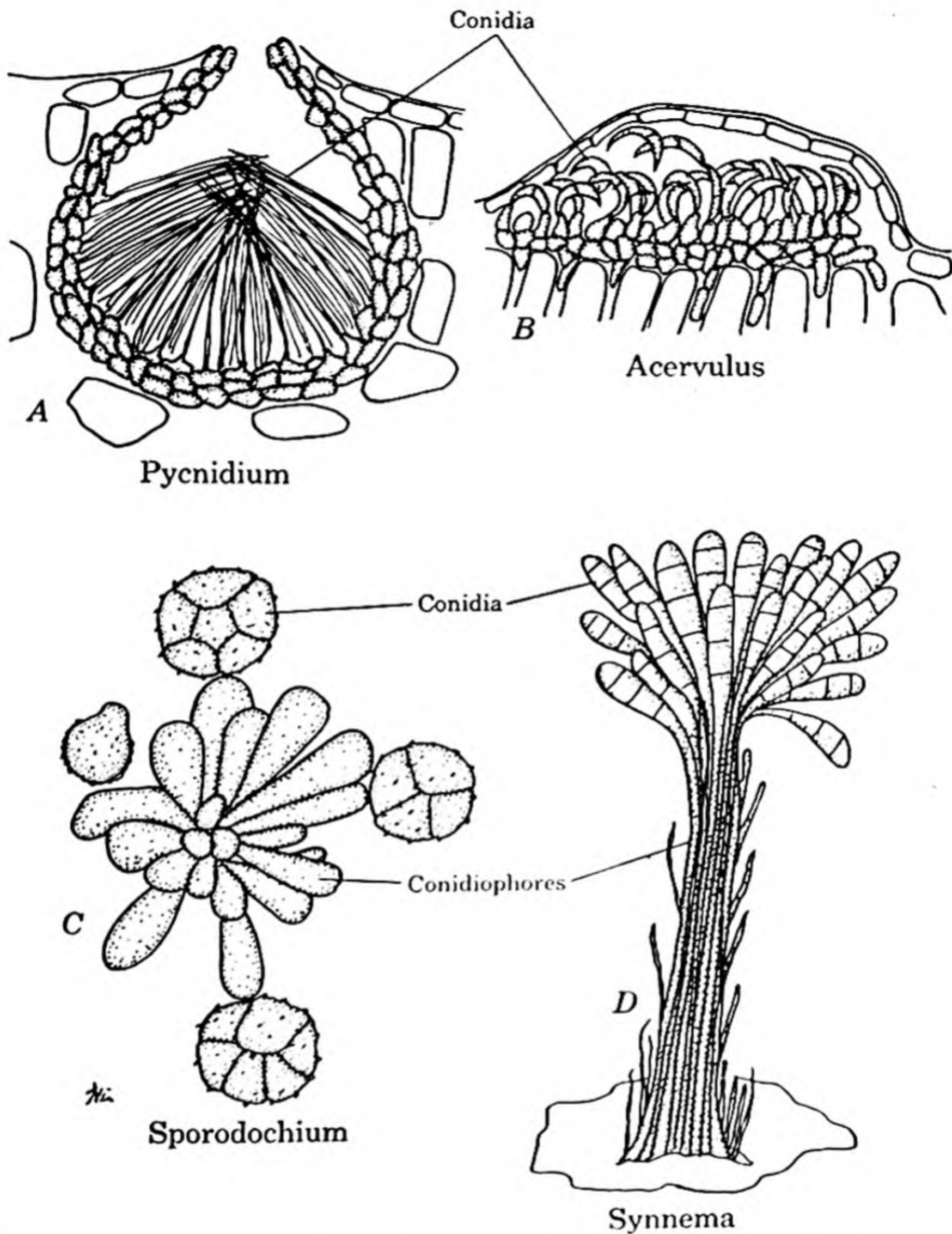


Figure 80. Four types of asexual fruiting bodies. *A. Septoria*. *B. Marssonina*. *C. Epicoccum*. *D. Arthrobotryum*. *D*, redrawn from Saccardo, in Engler and Prantl, 1900, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^{oo}, Wilhelm Engelmann, Leipzig.

which develops into the ascus. Meiosis of the diploid, zygote nucleus occurs almost immediately after fusion, and results in the production of four haploid nuclei. These four nuclei divide once more mitotically, and form eight nuclei which become incorporated into the eight ascospores typically produced in the ascus. This is, in brief, the developmental process of the asci and ascospores, which are the characteristic structures of the Ascomycetes.

We are now ready to examine the methods which Ascomycetes employ to bring two compatible nuclei together. The most common of these are the following:

(1) *Gametangial Copulation*. This method may be regarded as similar to that found in the Zygomycetes. Two similar gametangia touch at their tips or coil around each other and fuse, the fusion cell developing into the ascus. No dikaryotic phase is developed in such species, karyogamy taking place immediately after plasmogamy. In the yeasts, which are unicellular, the somatic cells themselves act as gametangia; two of them fuse and form a unicellular zygote which becomes transformed directly into the ascus, as we shall see later.

(2) *Gametangial Contact*. Some species produce morphologically differentiated uninucleate or multinucleate gametangia. These are designated as antheridia and ascogonia (sing. ascogonium; Gr. *askos* = sac + *gennao* = I give birth), the latter being the female structures from which the asci eventually develop. The gametes are reduced to undifferentiated protoplasts, the male nucleus passing from the antheridium into the ascogonium through a pore developed at the point of contact between the two gametangia. No fertilization tubes are formed, but the ascogonium is often provided with a trichogyne (Gr. *thrix* = hair + *gyne* = woman, female) which receives the male nucleus.

In some Ascomycetes the antheridia, although formed, have lost their function; in others no antheridia are formed. Either the ascogonia of such species receive nuclei from their trichogynes, which pair with the ascogonial nuclei, or the ascogonial nuclei themselves form functional pairs.

(3) *Spermatization*. In some species which form no antheridia, nuclei reach ascogonia by means of spermatia, microconidia, or conidia. Spermatia are minute, spherical or bacillary, specialized, uninucleate, male sex cells which become attached to the receptive organs—be they trichogynes or somatic hyphae—and empty their contents into them. The spermatial nuclei migrate to the ascogonium

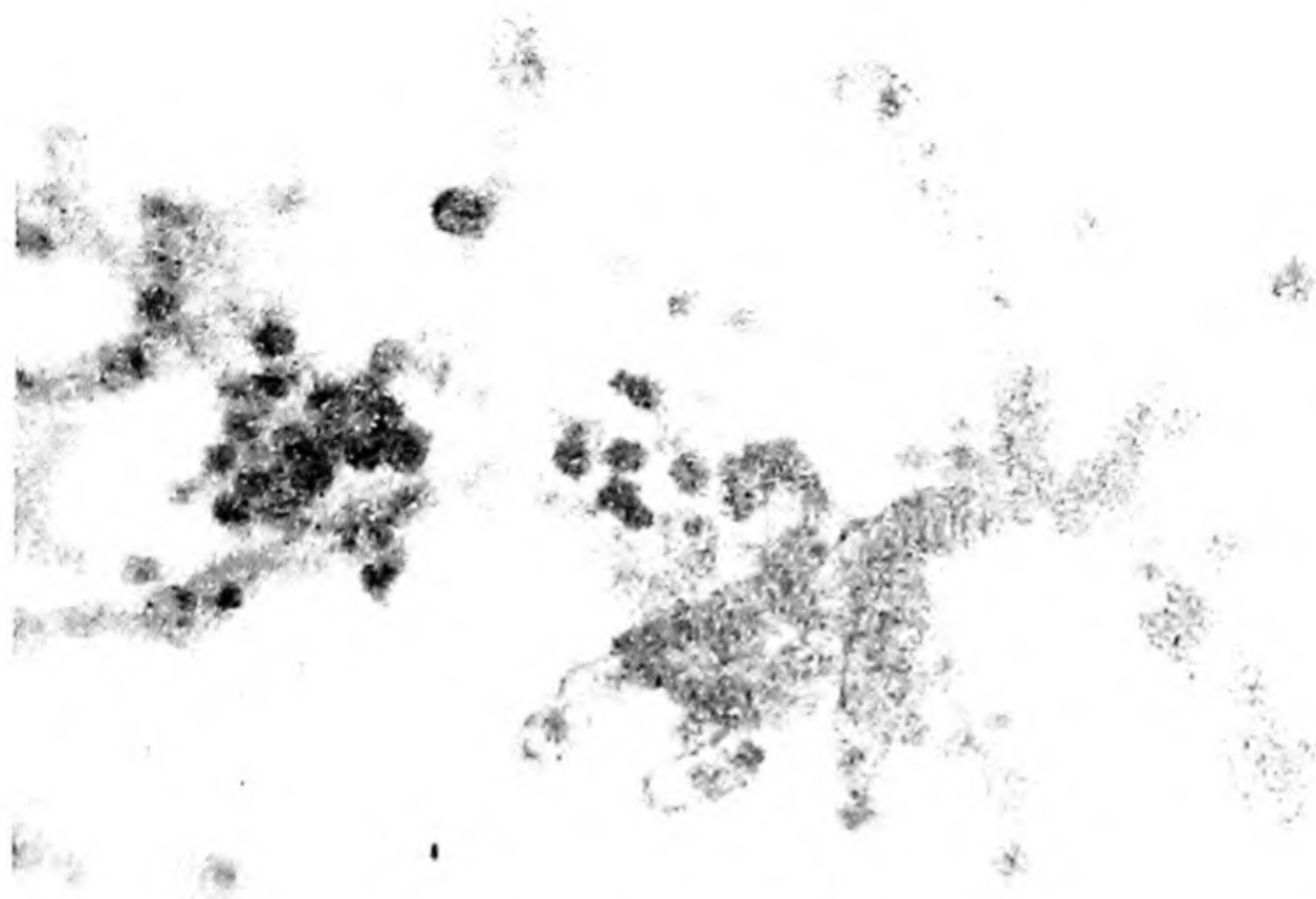


Figure 81. Microconidia and microconidiophores. (*Gelasinospora calospora* var. *autosteira*.) Courtesy Goos, 1959, *Mycologia*, 51:416-428.

through the septal pores. Spermatia become detached from or slip out of the parent hyphae and are carried by some means such as insects, wind, or water to the receptive organs. The hypha which produces spermatia is called the **spermatophore** (Gr. *spermaton* = little seed + *phoreus* = bearer).

Microconidia (Figure 81) are minute conidia which behave as spermatia but are also capable of germinating and giving rise to mycelium. Conidia and oidia may also function as spermatia by attaching themselves to the receptive organs and emptying their contents into them.

(4) **Somatogamy.** In some Ascomycetes fusion of somatic hyphae of two compatible mycelia takes place, and the nuclei migrate to the ascogonia through the septal perforations.

There are strong indications that a complicated hormonal mechanism operates in initiating plasmogamy, at least in some Ascomycetes. We know, for example, that trichogynes are attracted to compatible male sex cells (spermatia, microconidia, oidia) and will

change their direction of growth in response to the proximity of such cells (Backus, 1934; Zickler, 1953; Bistis, 1957; Goos, 1959).

Compatibility. With respect to compatibility the Ascomycetes fall into two groups: (1) homothallic species in which all individuals are self-compatible and are capable, therefore, of forming asci by themselves, and (2) heterothallic species in which two compatible individuals must be mated before asci are formed. In the latter species compatibility is determined by a pair of genes Aa (see page 29) which segregate at meiosis just before ascospore formation. As a result, four ascospores in each ascus normally carry gene A and the other four gene a . Each ascospore therefore will produce mycelium in which all the nuclei will carry but one factor, A or a . Both types of sex organs (antheridia or spermatia, and ascogonia) formed on this mycelium will carry the same factor and therefore will be unable to mate among themselves. Two thalli of different genetic make-up must be brought together so that an A antheridium (or spermatium) may come in contact with an a ascogonium, and vice versa. The dikaryons formed by the mating of two such compatible thalli would have the formula $A + a$, and the zygote nuclei the formula Aa . This one-locus, two-allele type of compatibility is called **bipolar heterothallism**.

Life Cycle Pattern. Although the life cycles of individual Ascomycetes vary in their details, the general pattern is the same in the class as a whole. Some of the important deviations which exist, especially in the primitive groups (Hemiascomycetidae), will be taken up in the following chapter, which deals with these fungi.

The mycelium of an ascomycete begins with the germination of the ascospore. One or more germ tubes issue from the spore as the nucleus or nuclei of the spore divide and their progeny distribute themselves in the growing hypha. Soon after growth is initiated, septa are laid down, branching takes place, and the germ tube develops into the mycelium.

In a great many Ascomycetes, the vigorously growing mycelium soon begins to form conidiophores characteristic of the species, which bear conidia. Conidia are usually termed summer spores because they are produced during the growing season. The same mycelium will continue to bear conidiophores as long as conditions are favorable. Since the production of these structures is a rapid process, many crops of conidia are borne in a single season. The conidia, produced in enormous numbers, are responsible for the propagation and dissemination of the species. Conidia are generally multinu-

cleate. Under favorable conditions they germinate each by a germ tube, and produce mycelium which is in all ways similar to that produced by the germination of the ascospores. In this way, a large number of asexual generations are produced during the growing season.

The same mycelium which produces the conidia later produces the asci. At certain places, the mycelium produces ascogonia. These may be uninucleate or multinucleate, depending on the species. Compatible nuclei are now brought to the ascogonia by one or more of the methods discussed on pages 224–225. Figures 82A, B, C show the contact of an antheridium and an ascogonium and the passage of the antheridial nuclei into the trichogyne and eventually into the ascogonial base. Exactly what happens after the nuclei have entered the ascogonium is a matter of controversy. In *Pyronema omphalodes*, the species on which this discussion is chiefly based, it has long been thought that, once in the ascogonial base, antheridial and ascogonial gamete nuclei approach each other in pairs (Figure 82C), but Miss Irene Wilson (1952) detected no regular pairing of the nuclei at this stage. At any rate we are quite certain that antheridial and ascogonial nuclei, paired or not, *do not fuse* at this point.

The stimulus of the sexual act causes the ascogonium to produce a number of papillae just opposite groups of nuclei located in the periphery of the ascogonium. The ascogonial walls appear to be thinner at these points. As these papillae enlarge, nuclei from the ascogonium begin to pass into them one by one. Eventually the papillae elongate into **ascogenous hyphae** (Figure 82D) in which a leading pair of nuclei can be detected, followed often by a second pair. The nuclei in the ascogenous hyphae and those still in the ascogonium soon undergo simultaneous mitosis. Septa are now formed in such a way that the tip cell of the ascogenous hypha is uninucleate (Wilson, 1952) and is followed by a series of binucleate cells which contain non-sister nuclei. It is probable that one nucleus in each binucleate cell of the ascogenous hyphae is ascogonial in origin and the other antheridial.

In a large number of Ascomycetes, one of the binucleate cells of the ascogenous hypha elongates and bends over to form a hook or crozier (Figure 82E). The two nuclei in this hooked cell divide in such a way that their spindles are oriented more or less vertically and parallel to one another (Figure 82F), so that two of the daughter nuclei—one from each spindle and, therefore, of different origin—

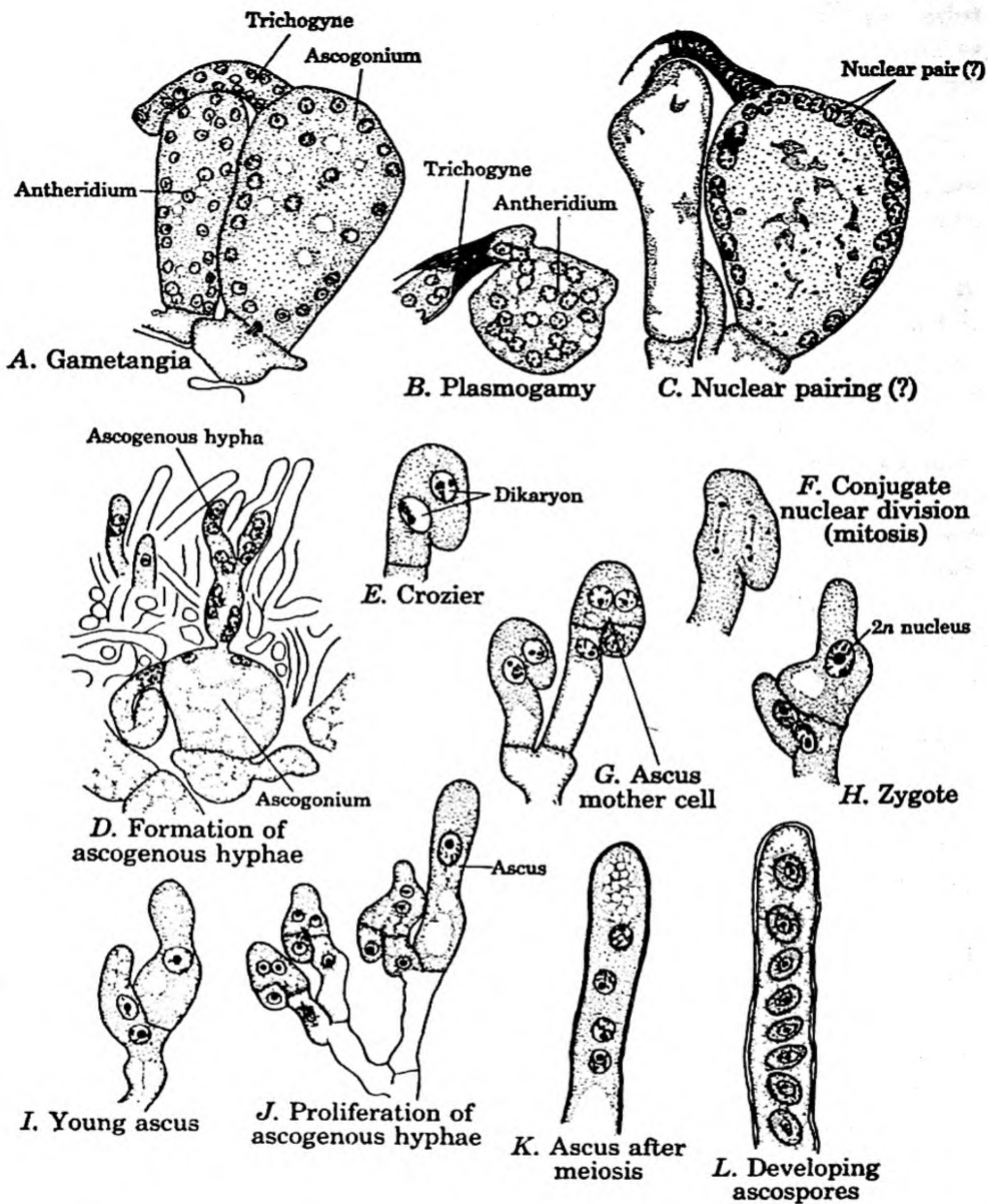


Figure 82. Sexual reproduction and ascus development in the Ascomycetes as exemplified by *Pyronema omphalodes*. Redrawn from Claussen, 1912, *Zeitschr. Botanik*, 4:1-64.

are close to one another at the bend of the hook, while one of the other two nuclei is located at the tip and one near the basal septum of the hook. Two septa are laid down, separating the hook into three cells (Figure 82G). The tip and basal cells are uninucleate, one containing an antheridial and one an ascogonial nucleus; the crook cell is binucleate. *This binucleate crook cell is destined to become the ascus and is termed the ascus mother cell.*

Karyogamy takes place in the ascus mother cell soon after the septa are formed in the hook, and the young ascus with its diploid, zygote nucleus begins to elongate (Figure 82H). The zygote nucleus soon undergoes meiosis, which results in four haploid nuclei (Figure 82K), each of which divides mitotically and forms eight nuclei in all. By a special process known as free cell formation a portion of the cytoplasm surrounding each nucleus now becomes enveloped by a wall, and the eight uninucleate cells thus formed mature into ascospores (Figure 82L). The portion of the cytoplasm left outside the spore walls probably serves as nourishment for the developing ascospores, and in many cases may deposit various external markings on the ascospore walls. Thus, eight uninucleate, haploid ascospores are typically formed as the result of plasmogamy (passage of the antheridial nuclei into the ascogonium), karyogamy (fusion of the nuclei in the ascus mother cell), and meiosis.

In most species of Ascomycetes developing according to the above pattern, each ascogenous hypha branches and rebranches in various ways, and produces a cluster of asci. This is often accomplished as follows: the crook cell elongates into a new hook instead of developing directly into an ascus, and the tip and basal hook cells fuse and form another hook by the side of the first. This process may be repeated several times, forming a cluster of hooks, the crook cells of which finally develop asci (Figures 82H, I, J).

Before you begin a study of Ascomycetes, it is important that you have a clear understanding of the method of ascus and ascospore formation just described. Here are some important reference points you should remember.

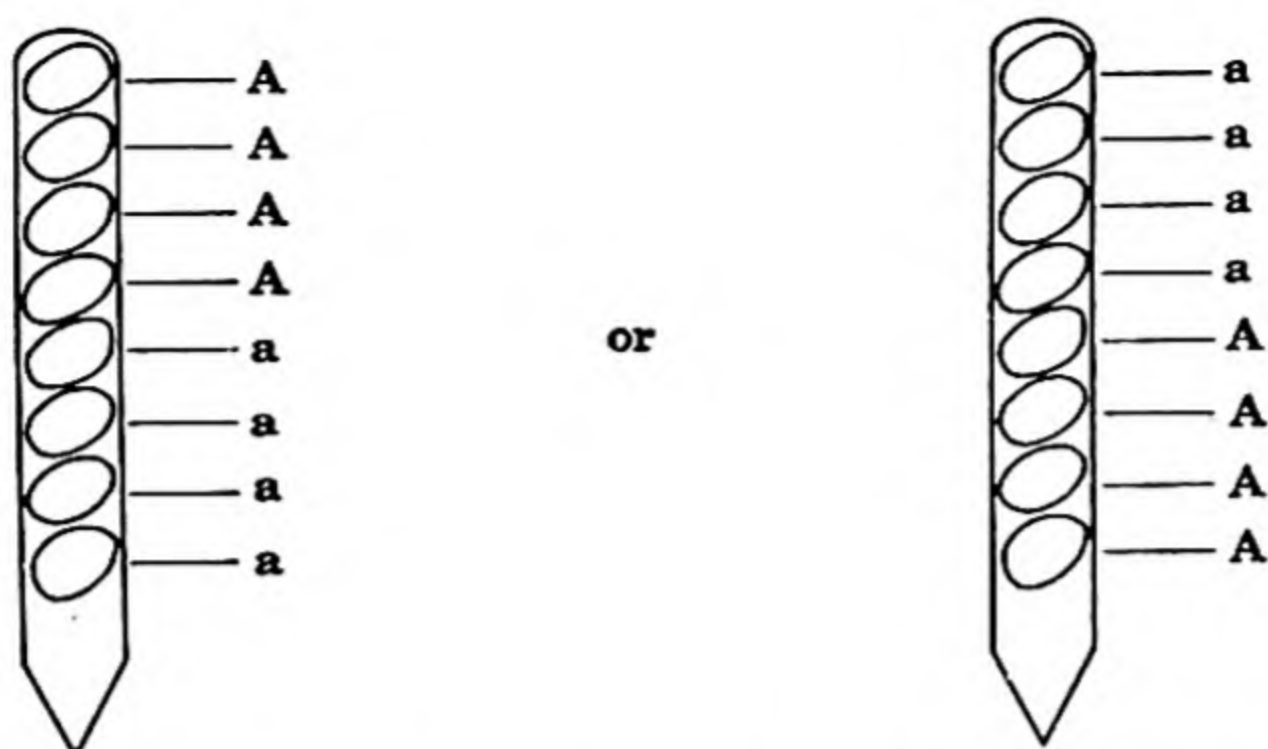
1. Nuclei pass from the antheridium into the ascogonium during plasmogamy.
2. Karyogamy occurs considerably later, in the ascus mother cell.
3. The zygote nucleus is the only true diploid structure in the entire life history of an ascomycete, but several cells are dikaryotic in the ascogenous hyphae. Plasmogamy precedes the di-

- karyotic phase and, in a way, initiates it; karyogamy produces the diploid phase, which, however, is of very short duration.
4. Whereas karyogamy is considerably delayed after plasmogamy has occurred, meiosis follows karyogamy immediately.
 5. Meiosis precedes ascospore formation so that the ascospores are haploid. Before ascospore formation, segregation of factors takes place in the ascus mother cell, which develops into the young ascus.
 6. Ascospores are usually uninucleate when young. As a rule they remain so, but in some species the nucleus divides and the mature ascospore is binucleate. In other species the ascospore becomes multinucleate, and then septa are formed separating the nuclei into separate cells. All nuclei in such spores carry the same haploid gene complex, since they are all descendants of a single haploid nucleus. Some species produce but four instead of eight ascospores in each ascus. Such ascospores are binucleate from the first because during ascospore formation a wall develops around a pair of nuclei instead of around each single nucleus in the ascus.

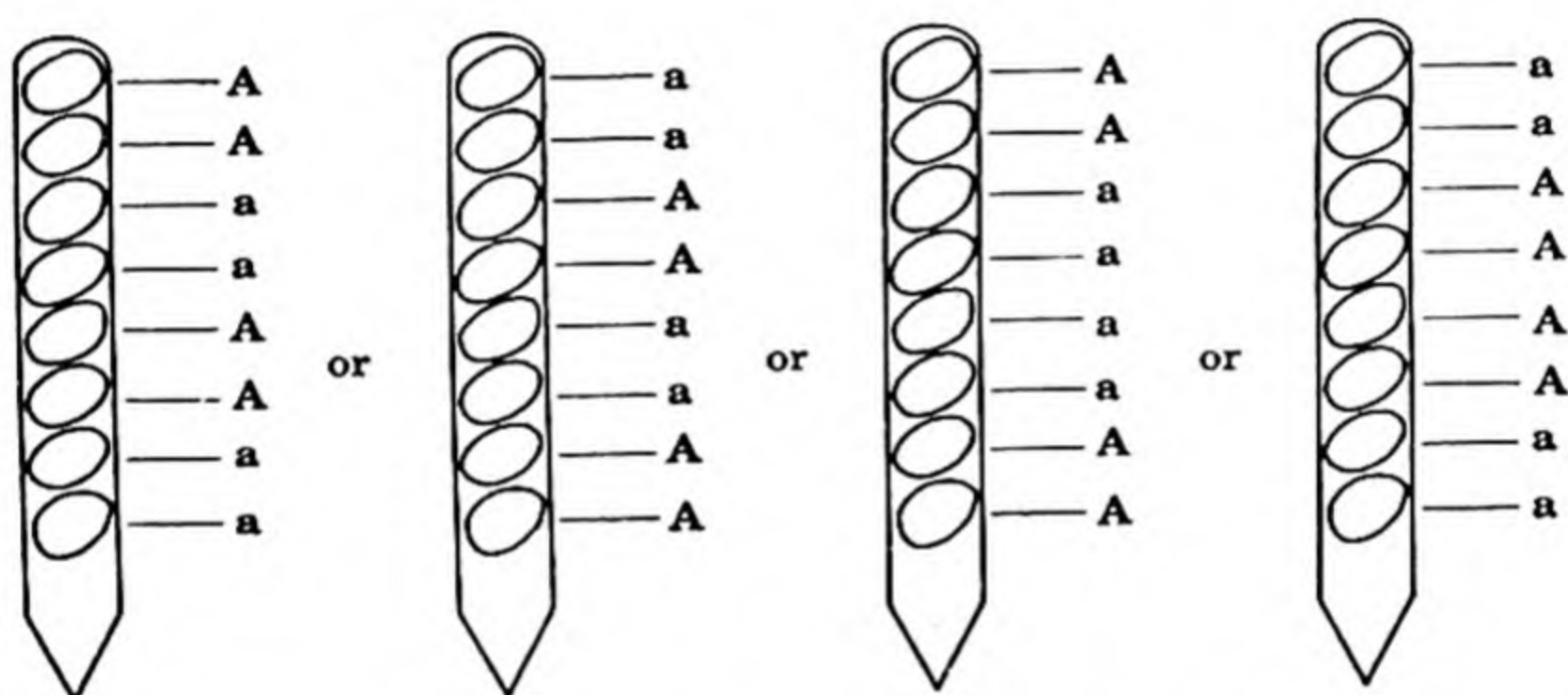
In some Ascomycetes the male gametangium, if indeed it is formed at all, does not function. In such species the nuclei present in the ascogonium pass into the ascogenous hyphae. Development is normal thereafter.

In accordance with this developmental scheme, the spores in each ascus are actually formed in pairs, each of the four pairs representing a part of the original tetrad resulting from meiosis of a single diploid nucleus. In species in which the asci are cylindrical and the spores are arranged in a series, segregation of characters can be studied as it occurs, the arrangement of the ascospores actually representing the arrangement of the chromosomes during meiosis. This can be illustrated by the way the mating type factor (for example) segregates in heterothallic species.

You will remember that in the heterothallic Ascomycetes the mating type is of the one-locus, two-allele pattern. Thus, an A nucleus fuses with an a nucleus, and of the ascospores in each ascus four carry the A factor and four the a. By isolating the individual spores from an ascus *in the order in which they occur* and mating the mycelia resulting from them in all possible combinations, we can determine how segregation of mating type occurs. If segregation occurs in the first meiotic division we will have:



If segregation occurs in the second meiotic division, the result will be:



The foregoing is true, of course, not only of mating type, but of any character inherited in the same manner.

The implications of the above to genetic research are tremendous. The discovery of the ascomycete *Neurospora*, particularly suited to genetic analysis, by B. O. Dodge and Cornelius Shear (Shear and Dodge, 1927) opened up a new era in the study of inheritance. Mycologist Dodge carefully laid down the foundations of *Neurospora* genetics through a series of research papers, and on this firm basis geneticists and biochemists built the new sciences of haploid genetics and biochemical genetics.

Asci and Ascospores. In the large majority of the Ascomycetes the asci are elongated, either club-shaped or cylindrical. But globose or ovoid asci are characteristic of some groups and rectangular asci of others (Figure 83). Ordinarily, the ascus represents a single cavity in which the ascospores are formed. Septate asci have been re-

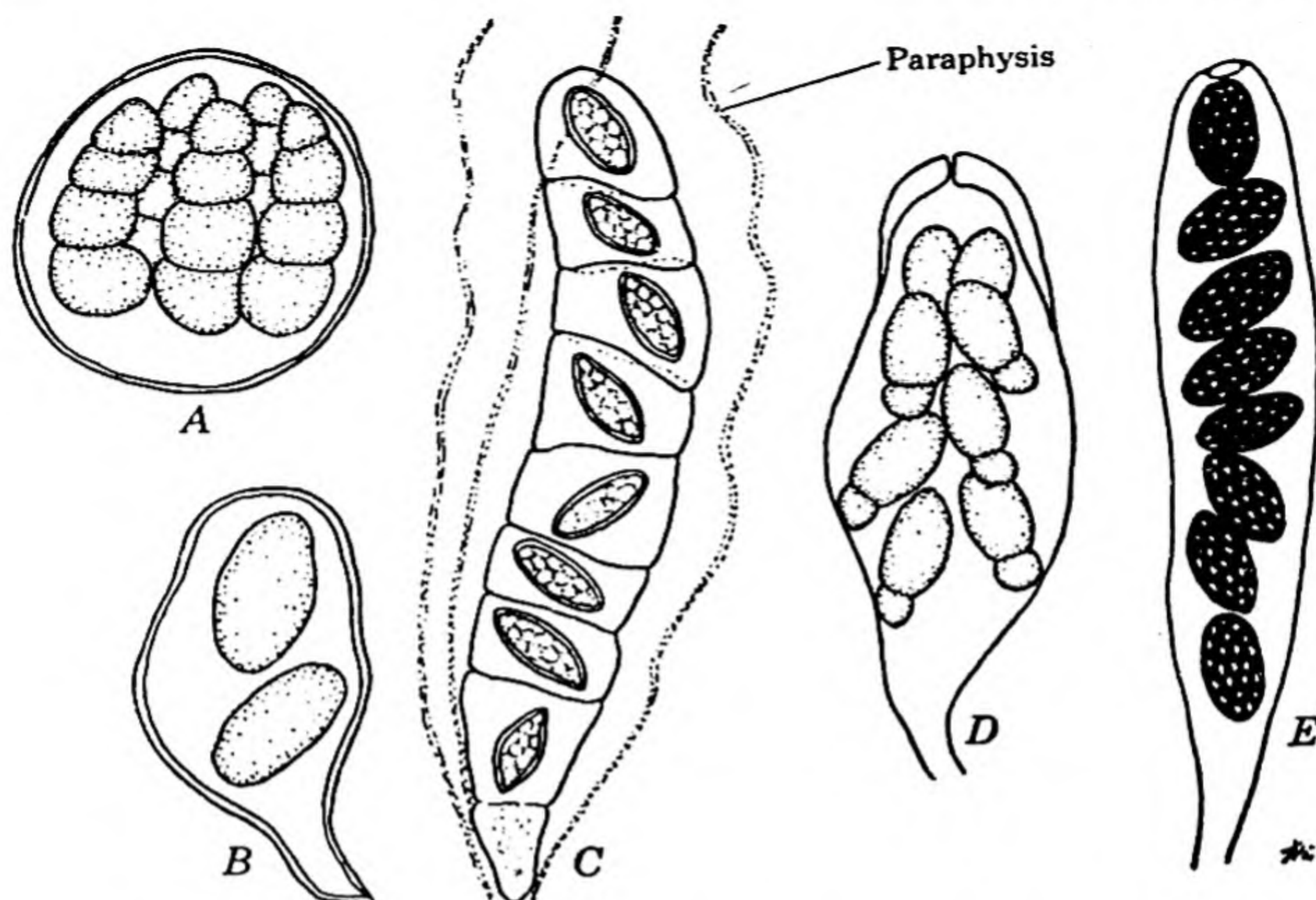


Figure 83. Various types of asci. A. Globose. B. Broadly ovate with stalk. C. Septate. D. Clavate. E. Cylindric. A, redrawn from Burkholder, 1917, *Cornell Univ. Agr. Exp. Sta. Bull.*, 395:157-183; C, redrawn from Stevens, 1927, *Ill. Biol. Monogr.*, Vol. XI, No. 2.

ported for one species (Stevens, 1927; Crouch, 1930), but this report needs confirmation. Asci may be stalked or sessile; they may arise from a common fascicle and spread out like a fan, or they may arise singly at various levels within the fruiting body. A definite layer of asci, whether naked or enclosed in a fruiting body, we call a **hymenium** (pl. *hymenia*; Gr. *hymen* = membrane). Sterile, elongated hairs, arising between the asci, often form a part of the hymenium. These structures, which are thought to aid in the dissemination of the asci and ascospores, are called **paraphyses** (sing. **paraphysis**; Gr. *para* = beside + *physis* = a being, a growth) (Figure 83C).

One of the most important features of ascus morphology, now proposed as the basis for classification of the Ascomycetes, is the structure of the ascus wall. In general, two types of asci are recognized: the **unitunicate** (L. *unus* = one + *tunica* = skin, tunic) and the **bitunicate** (L. *bis* = twice + *tunica* = skin, tunic).

The relatively thin wall of the unitunicate ascus (Figures 87A-D) consists of two thin layers forming what appears to be a single wall,

which may be uniform in thickness, but which, more often than not, is conspicuously thickened at the apex. Asci with a thickened apex are usually provided with a pore or canal through which the ascospores escape. In the bitunicate ascus (Figure 87E) there are two distinct wall layers, a rigid outer and an extensible inner wall. At maturity the outer wall breaks below the tip. The inner wall absorbs water and elongates. It has a pore at the apex through which the ascospores are forcibly ejected. For a more complete discussion of ascus structure consult Luttrell (1951), Chadeaud (1954, 1960), and Dennis (1960).

Ascospores vary greatly in size, shape, color, and other characteristics. In size, they vary from minute to more than $1000\ \mu$ in length; in shape, from globose to thread-like; in color, from colorless to black; in number of cells, from one to many (Figure 84). We use these characteristics of the ascospores as criteria in the classification of genera and species of Ascomycetes.

The Ascocarp. With relatively few exceptions, Ascomycetes produce their asci in fruiting bodies called **ascocarps** (Gr. *askos* = sac + *karpos* = fruit). In general there are five major categories of Ascomycetes, separated according to the way they bear their asci: (1) those which bear naked asci without any fruiting body (Figure 85A); (2) those which produce their asci inside a completely closed ascocarp called a **cleistothecium** (pl. **cleistothecia**; Gr. *kleistos* = closed + *theke* = case) (Figure 85B); (3) those whose ascocarp, the **perithecium** (pl. **perithecia**; Gr. *peri* = around + *theke* = case), is more or less closed, but at maturity is provided with a pore through which the ascospores escape (Figure 85C); (4) those which produce their asci in an open ascocarp, called an **apothecium** (pl. **apothecia**; Gr. *apotheke* = storehouse) (Figure 85D); and (5) those which form their asci directly in a cavity (locule) within the stroma. The stroma itself thus forms the wall of the ascocarp in such species. We call such a structure an **ascostroma** (pl. **ascostromata**; *ascus* + *stroma*) (Figure 132M). In addition, various modifications of these structures result in a number of intermediate forms difficult to classify. We shall discuss ascocarp structure in much more detail in subsequent chapters.

In some Ascomycetes the ascocarp develops as a response to the sexual stimulus. After plasmogamy has taken place, the somatic hyphae around these organs are activated to interweave into a prosenchymatous or pseudoparenchymatous tissue which forms the perithecium or the apothecium. Perithecia or apothecia may consist of either type of tissue mentioned, or of both types. In other Ascomy-

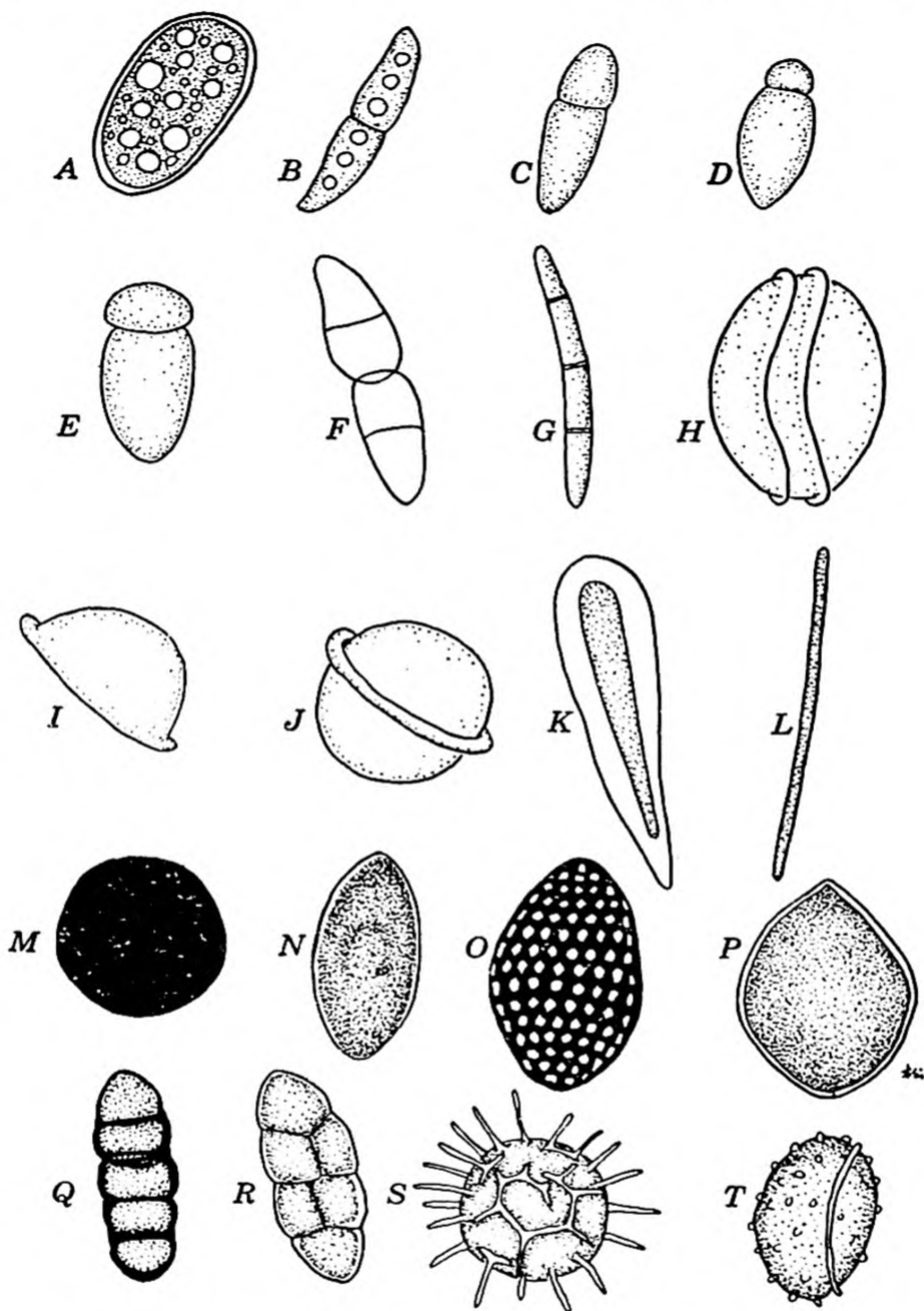


Figure 84. Various types of ascospores. *H*, by permission, from *A manual of the aspergilli*, by Charles Thom and K. B. Raper, 1945, Williams & Wilkins Co., Baltimore; *Q*, redrawn from Stevens, 1916, *Ill. Biol. Monogr.*, Vol. II. No. 4; *S*, *T*, redrawn by permission from *The North American cup fungi (Operculates)*, by F. J. Seaver, 1942, published by the author, New York.

cetes, the ascocarp begins to develop first, and the sexual organs are formed from the hyphae already within the developing ascocarp. In either case, the ascocarp develops from somatic tissue.

Ascocarps may be formed singly or in groups. They may be superficial, erumpent (pushing through the tissues of the host), or deeply embedded in the substratum. The substratum may be composed en-

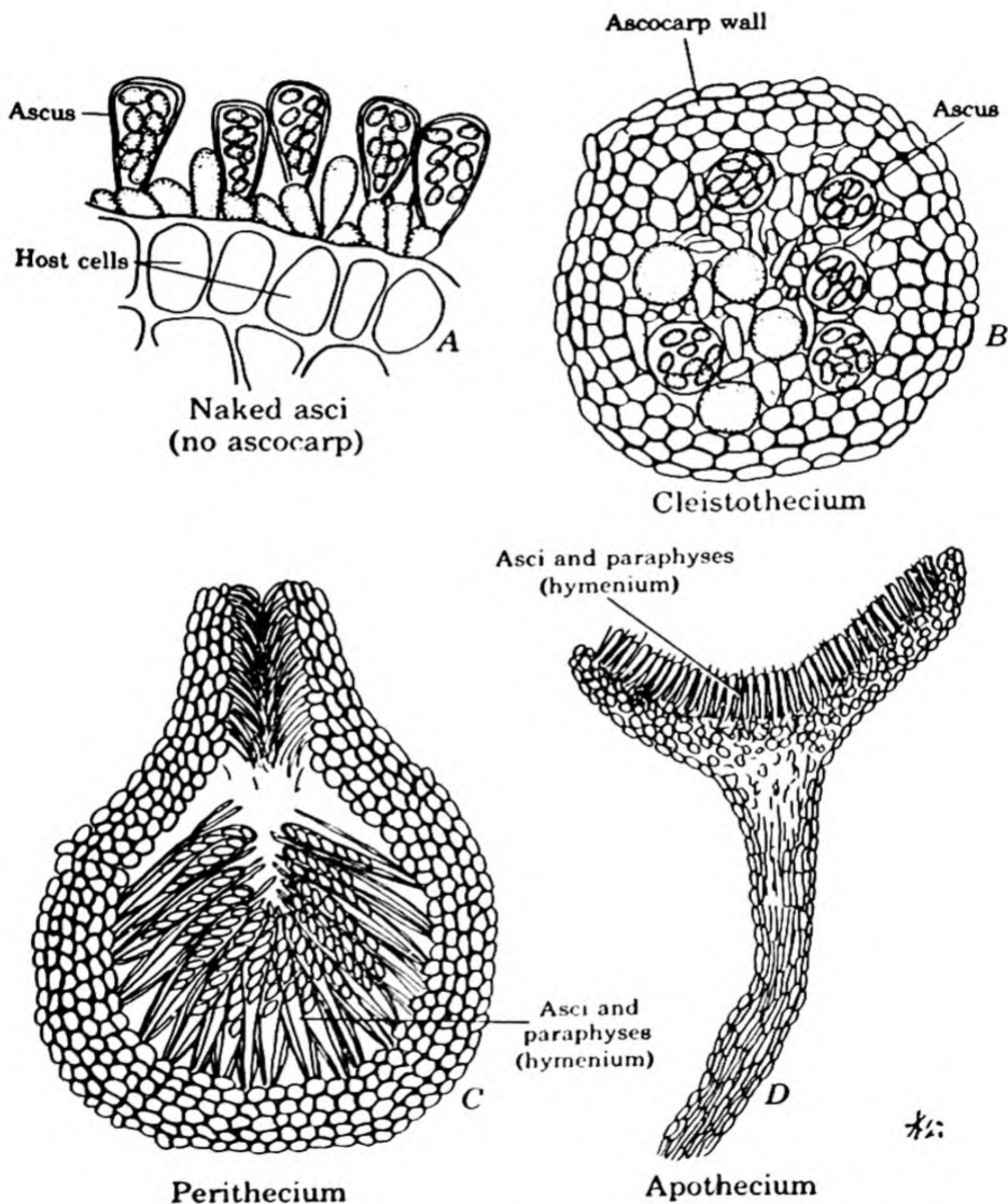


Figure 85. Four ways in which Ascomycetes bear their asci.

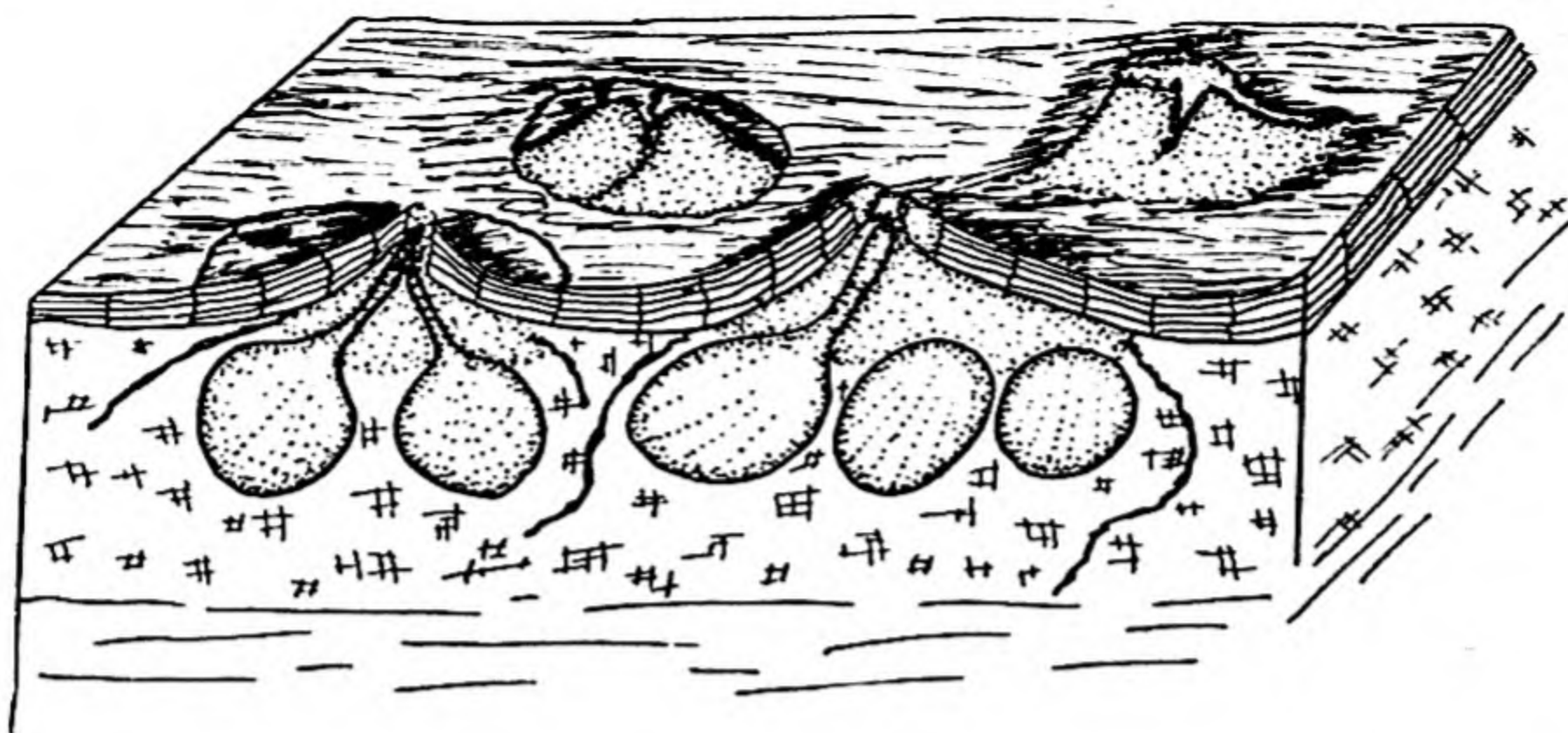


Figure 86. Section of stroma, showing embedded ascocarps. Redrawn by permission from *A revision of Melanconis, Pseudovalsa, Prosthecium and Titania*, by Lewis Wehmeyer, 1941, University of Michigan Press, Ann Arbor.

tirely of host tissue, or it may be a hyphal stroma on or in which the ascocarps form. The concept of a stroma is a bit difficult for beginning students to understand. Visualize a stroma as being a mattress or cushion of closely woven hyphae which in themselves are somatic in nature, but which very often give rise to fruiting bodies either on the surface of the stroma or inside it. If the ascocarps are on the surface, they are easily distinguished from the stroma; but, if they are embedded within the stroma, only their pin-point openings which protrude from the surface can be detected without making a vertical section of the stroma through an ascocarp (Figures 86, 118).

Release and Germination of Ascospores. When the ascospores are mature, some provision is generally made for their release and dissemination. In species which form no ascocarps, the release of the spores takes place by the bursting or the disintegration of the asci which are formed on the substratum. The spores are distributed by wind, water, insects, or other agencies. If the ascocarp is a perithecium or an ascostroma, it is provided at the top with a pore through which the ascospores are liberated. In some orders, however, the ascocarp is completely closed and the ascospores are liberated only upon the partial or complete disintegration of the ascocarp. Apothecia are open at the top when mature, except for a few hypogean forms which remain completely closed until disintegration sets in or until the ascocarps are broken by animals which feed upon them.

In a large number of Ascomycetes, ascospores are forcibly ejected from the ascus by a puffing action. You can easily see these clouds of ascospores; they have often been photographed as they are puffed out of an ascocarp. In some species such as the morels, puffing is accompanied by a hissing sound. Ascospores are ejected either through the bursting of the ascus at the tip or through a natural pore, slit, or cap-like operculum hinged at one end (Figures 87A–E). Slight differences in the moisture content of the air immediately surrounding the ascocarp are among the factors responsible for puffing. Temperature, light, and air currents also affect puffing. This action is repeated several times by the same ascocarp until all the ascospores have been freed.

Ingold (1954) has observed that in Ascomycetes which produce asymmetrical spores, such as ovoid spores, the blunt end of the spore is always oriented toward the tip of the ascus, and he discusses the possible advantage of such orientation in increasing the initial velocity of the ascospore at the time of its escape from the ascus.

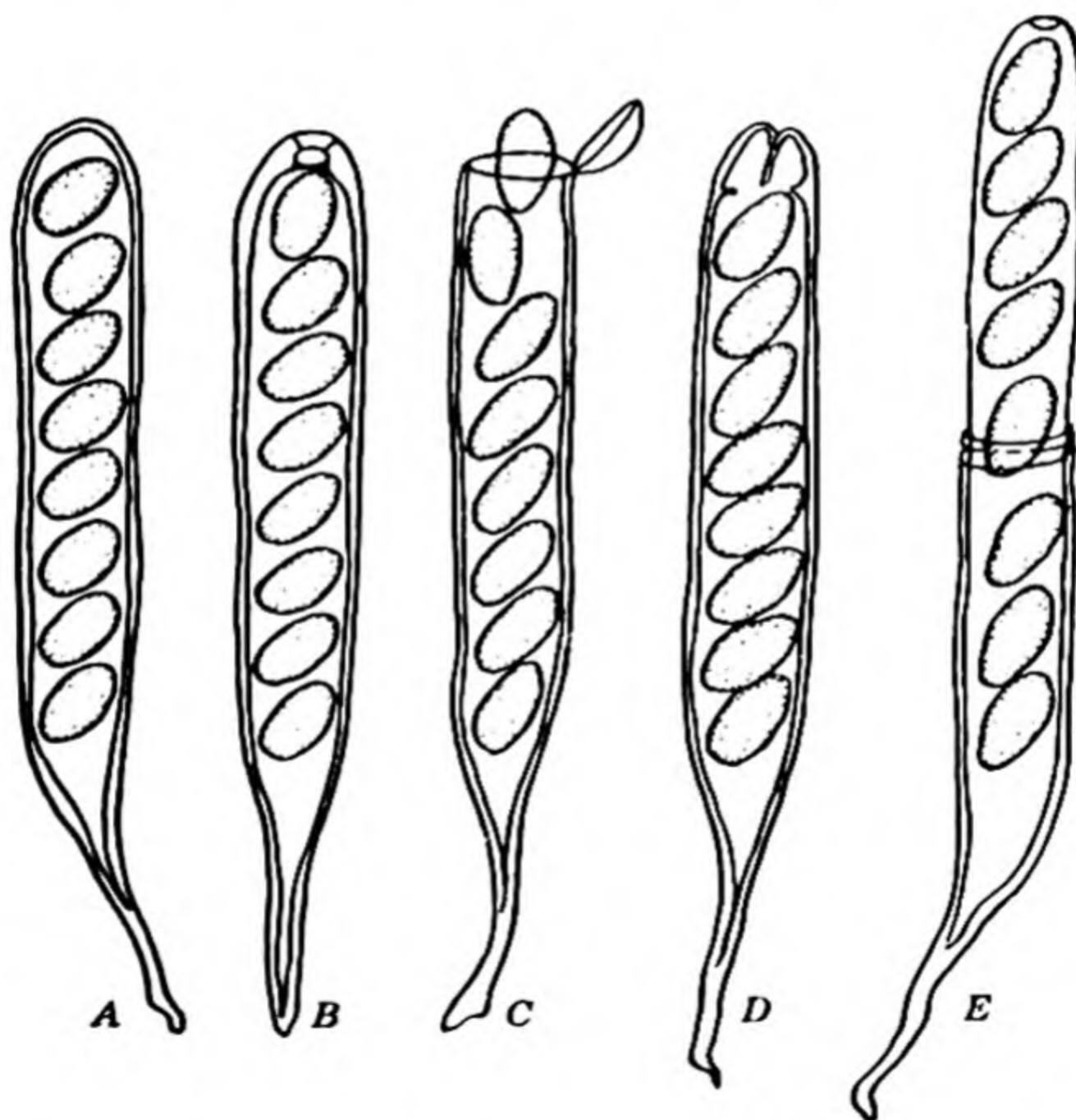


Figure 87. Various types of ascus openings. A. No opening. B. Ascus pore. C. Operculum. D. Slit. E. Dehiscence of bitunicate ascus with pore at tip of inner, expanded wall.

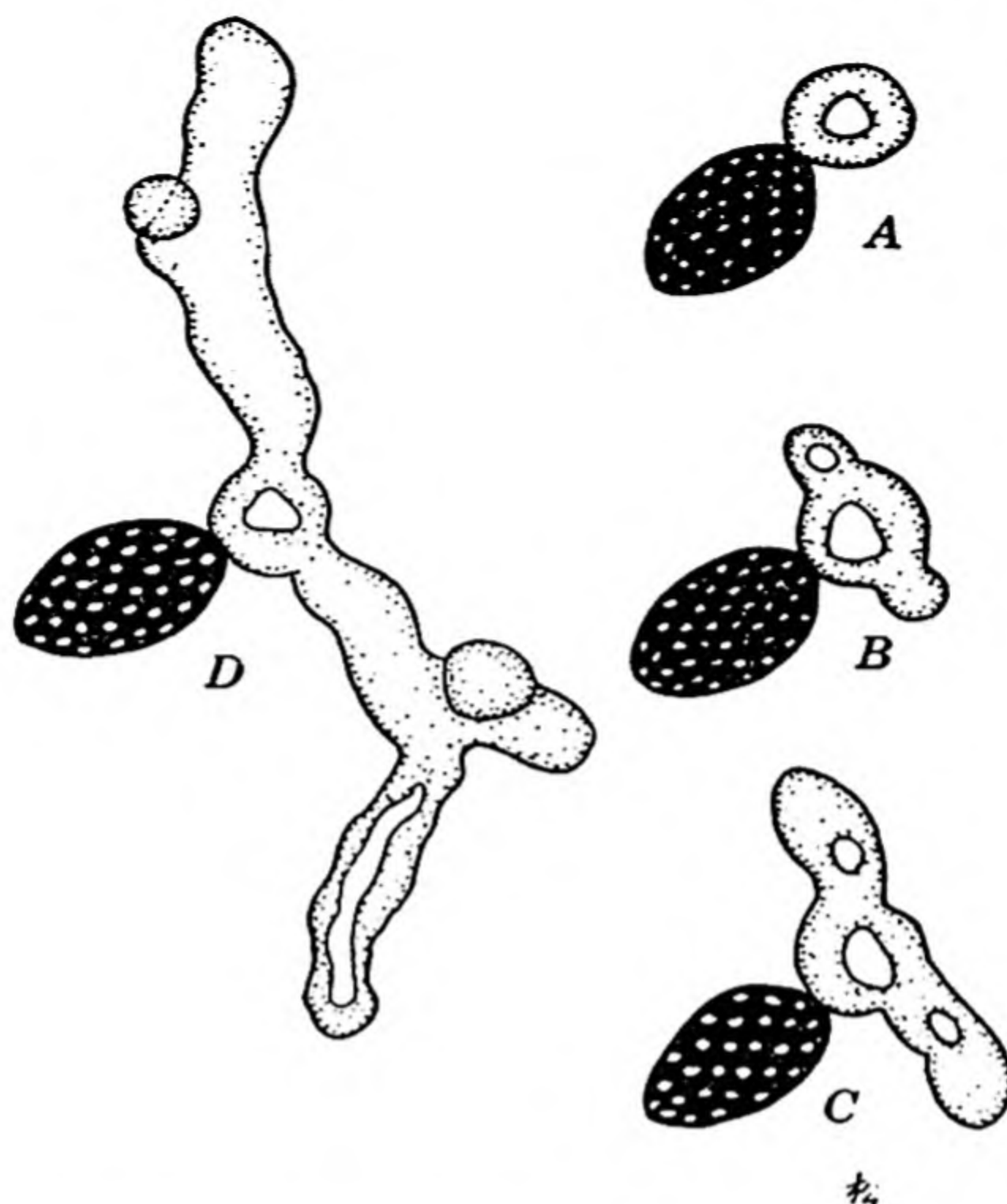


Figure 88. Four stages in ascospore germination, drawn at 30-minute intervals. (*Gelasinospora calospora* var. *autosteira*.)

Under favorable conditions ascospores germinate by one or more germ tubes which develop into a septate mycelium typical of the species (Figure 88). Multicellular ascospores may produce a number of germ tubes, one from each cell. In many yeasts and some other fungi the ascospores multiply by budding instead of producing germ tubes.

Given some moisture and a temperature somewhere around 20° C., most ascospores will germinate as soon as they are mature. The ascospores of some species, however, require special conditions for germination, as shown by the difficulty we experience in germinating them in the laboratory. Special treatment such as freezing, heating, or immersion in acid is necessary before the spores of some species can be induced to germinate.

Classification. The Ascomycetes are classified into three sub-classes on the basis of their ascocarps, the method of ascus formation, and the structure of their asci. The first of these sub-classes, the **Hemiascomycetidae**, sometimes also called **Protoascomycetidae**

is considered by most mycologists to be the most primitive. It includes those Ascomycetes which form no ascocarps and no ascogenous hyphae, but which bear naked asci. The other two classes produce their asci in ascocarps. The *Euascomycetidae* typically produce unitunicate asci in perithecia, apothecia, or cleistothecia. The *Loculoascomycetidae* form their ascospores in bitunicate asci which are borne in ascostromata.

KEY TO THE SUB-CLASSES OF THE CLASS ASCOMYCETES

- A. Asci arising naked; no ascogenous hyphae or ascocarps produced *Hemiascomycetidae*
- AA. Asci produced in ascocarps, mostly from ascogenous hyphae
 - B. Asci typically unitunicate, if bitunicate, then borne in an apothecium; ascocarps of various types *Euascomycetidae*
 - BB. Asci bitunicate; ascocarp an ascostroma *Loculoascomycetidae*

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12 sub-class HEMIASCOMYCETIDAE the yeasts and leaf-curl fungi

Introduction. The Hemiascomycetidae are either very primitive Ascomycetes or degenerate forms, depending on whether their structure is considered to be primitive or derived. The name **Hemiascomycetidae** or Protoascomycetidae is applied to them because most mycologists believe them to be primitive. Their simplicity of structure is shown by an often scant or totally lacking mycelium, by the direct formation of asci without the intervention of a system of ascogenous hyphae, and by the complete absence of ascocarps.

Classification. The Hemiascomycetidae include the yeasts and yeast-like organisms, a few mycelial saprobes growing on plant exudates, and the fungi which cause leaf-curl diseases on various plant hosts. There is considerable disagreement, even among specialists, concerning the division of this sub-class into orders and families. The most conservative view recognizes only two orders: Endomycetales and Taphrinales. But, whereas there is little or no quarrel concerning the Taphrinales, the same cannot be said about the Endomycetales. These are sometimes split into two, three, or more orders. In addition, another group of fungi, of very uncertain relationships, the Protomycetales, is sometimes included in the Hemiascomycetidae (Martin, 1961), but our knowledge of these is so fragmentary that we shall not attempt to discuss them.¹ As for the Endomycetales, until more information is available concerning them it seems best to adopt the most conservative view.

KEY TO THE ORDERS OF THE SUB-CLASS HEMIASCOMYCETIDAE

- A. Asci arising directly from zygotes each derived from the copulation of two cells, or parthenogenetically from single cells *Endomycetales*

¹ See Bessey, 1950; Gäumann, 1952; Spiltoir and Olive, 1955.

- AA. Asci arising from binucleate ascogenous cells which develop similarly to chlamydospores from the binucleate mycelium

Taphrinales

order ENDOMYCETALES

We place in this order those Hemiascomycetidae in which the zygote, derived from the copulation of two cells, becomes directly transformed into an ascus. In many forms a single cell becomes the ascus parthenogenetically, the sexual act being omitted altogether. In other forms the diploid zygote gives rise to a large number of diploid cells by budding, and these, in turn, develop into asci.

The Endomycetales concern us economically because they include the yeasts, so important in industry. The sub-division of this order into families is, as mentioned above, highly controversial. Not only does the number of families vary with the author, but the names and the limits of each family as well. We shall follow Martin (1961), who recognizes four families: Ascoideaceae, Endomycetaceae, Saccharomycetaceae, and Spermophthoraceae.

SIMPLE KEY TO THE FAMILIES OF THE ORDER ENDOMYCETALES

(Modified from G. W. Martin, 1961)

- | | |
|---|---------------------------|
| A. Asci multispored | <i>Ascoideaceae</i> |
| AA. Asci mostly 1–8 spored ¹ | |
| B. Mycelium abundant | |
| C. Plasmogamy by copulation of uninucleate gametangia | <i>Endomycetaceae</i> |
| CC. Plasmogamy by copulation of non-motile gametes released from gametangia | <i>Spermophthoraceae</i> |
| BB. Mycelium scanty or lacking | <i>Saccharomycetaceae</i> |

¹ In *Kluyveromyces polysporus*, which undoubtedly belongs to the Saccharomycetaceae, the ascus contains a large number of spores.

family ASCOIDEACEAE

The members of this family are of no economic importance. They inhabit exudates of plants in which they live saprobically. The Ascoideaceae are fungi with a well-developed, septate mycelium the cells of which are often multinucleate but may be uninucleate. Asexual reproduction takes place usually by means of conidia or oidia

produced from the somatic hyphae or from needle-shaped synnemata. Sexual reproduction is by copulation of two gametangia. The family, as treated here, includes three genera: *Ascoidea*, *Dipodascus*, and *Helicogonium*. Batra (1959) believes that the last two should be placed in a separate family (Dipodascaceae), but does not define clearly the two families as he conceives them. The very interesting genus *Ascocybe* (Wells, 1954) probably has its affinities with the Ascoideaceae. It produces asci on special ascophores which are apparently diploid (Wilson, 1961). No nuclear fusion takes place in the ascus, but meiosis precedes ascospore formation.

Dipodascus, the best known of these genera, includes three species: *Dipodascus albidus*, *Dipodascus uninucleatus*, and *Dipodascus aggregatus*. All three are homothallic.

Dipodascus albidus, a species which several mycologists have studied in culture, may serve as our example. The multinucleate, septate mycelium produces, side by side, two multinucleate gametangia which soon come in contact. At first similar morphologically, the gametangia soon differentiate into a larger and a smaller. The walls dissolve at the point of contact and the contents of the gametangia merge, the male nuclei from the smaller cell migrating into the larger, female gametangium. After copulation, karyogamy takes place only between two functional nuclei, one from each gametangium. The zygote nucleus now undergoes several divisions, and the female gametangium elongates into an ascus. As the zygote nucleus divides repeatedly and forms many new nuclei, the non-functional gametangial nuclei gradually disintegrate. Each nucleus (derived from the zygote), together with a portion of the adjacent cytoplasm, is now surrounded by a wall and develops into an ascospore. The ascus ruptures at the tip and releases the ascospores which then germinate into new hyphae. It is probable that the first two divisions of the zygote nucleus constitute meiosis.

Matters are somewhat simplified in *Dipodascus uninucleatus*, the hyphae and gametangia of which are uninucleate. The cycle is the same as in *Dipodascus albidus*, but *Dipodascus uninucleatus* has become simplified by the elimination, from the very beginning, of the non-functional, supernumerary nuclei (Figure 89). According to Batra (1959), asexual reproduction in *Dipodascus albidus* and *Dipodascus aggregatus* is by multinucleate oidia (arthrospores); in *Dipodascus uninucleatus* by yeast-like sprout cells (blastospores).

Dipodascus is a key genus in the phylogenetic scheme which seeks the origin of the Ascomycetes in the lower fungi. The fusion of the multinucleate gametangia of *Dipodascus albidus* is reminiscent of

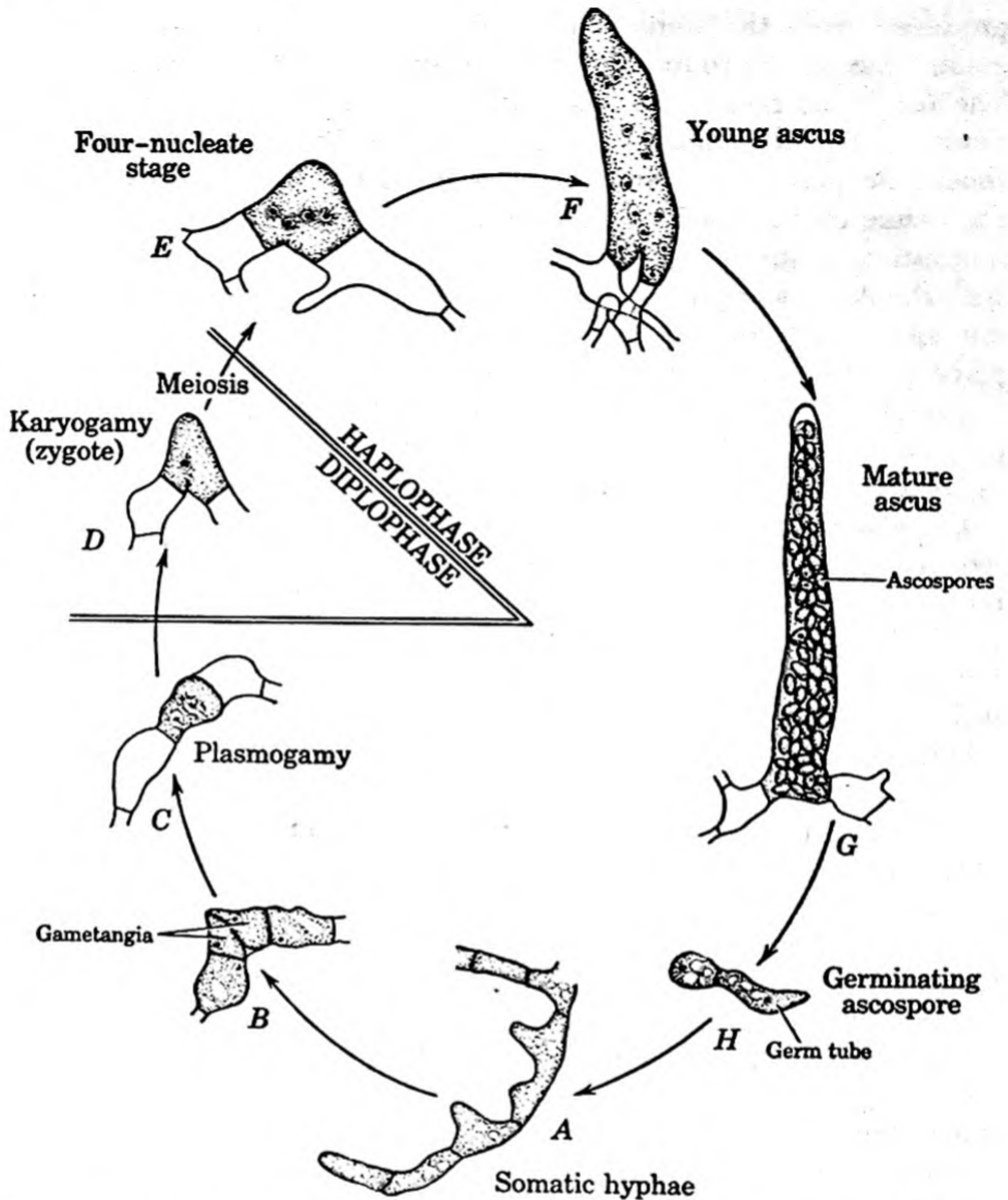


Figure 89. Life cycle of *Dipodascus uninucleatus*. B-H, redrawn from Miss Biggs, 1927, *Mycologia*, 29:34-44.

gametangial copulation in some of the Zygomycetes, and the multi-spored ascus has been homologized with the germ sporangium. A telescoping of the life cycle has eliminated the zygospore, in accordance with this theory, meiosis presumably taking place in the young "ascosporangium."

family ENDOMYCETACEAE

The Endomycetaceae differ from the Ascoideaceae in producing a small and generally definite (one to eight) number of ascospores in each ascus. The mycelium of these fungi is composed of well-developed, typical hyphae. The asci are formed from zygotes each of which develops from the fusion of two uninucleate gametangia or, in some instances, parthenogenetically. Asexual reproduction is by means of arthrospores or blastospores.

Eremascus, *Endomyces*, and *Endomycopsis* are three representative genera in this group. *Eremascus fertilis* produces abundant, well-developed mycelium composed of uninucleate cells (Figure 90A). Reproduction begins with two gametangia which originate as small branches of adjacent mycelial cells (Figure 90B). The nucleus of each cell divides, and one daughter nucleus enters the gametangium. Gametangial copulation (plasmogamy) takes place, followed by karyogamy (Figures 90C–E). The zygote thus formed is separated from the gametangial bases by septa, enlarges, and develops into an ascus. Three nuclear divisions, the first two of which we presume to be meiotic, result in eight nuclei around which eight ascospores develop (Figures 90F, G).

Neither *Eremascus* nor the related genera are of economic importance, but they are of interest in a discussion of ascomycetous relationships.

family SACCHAROMYCETACEAE

The Saccharomycetaceae are the yeasts. As used here, the term yeast refers to Ascomycetes which possess a predominantly unicellular thallus, which reproduce asexually by budding, transverse division (fission) or both, and which produce ascospores in a naked ascus, originating either from a zygote or parthenogenetically from a single somatic cell. Forms which are not known to produce ascospores, but which possess all other characteristics listed above, and which are not obviously related to other groups of fungi, are also included generally under the term yeast, for it is believed that many yeasts have lost their ability to form ascospores or that they may actually form them under conditions as yet unknown to us. We often refer to such organisms as the *asporogenous* yeasts (Gr. *a* = not + *sporos* = seed, *spore* + *gennao* = I give birth). We shall discuss them in Chapter 18 with the imperfect fungi.

The eminent French scientist, Professor A. Guilliermond, who devoted a lifetime to the study of yeasts and related forms, believed that the true yeasts have been derived from the mycelioid forms by reduction (Guilliermond, 1940).

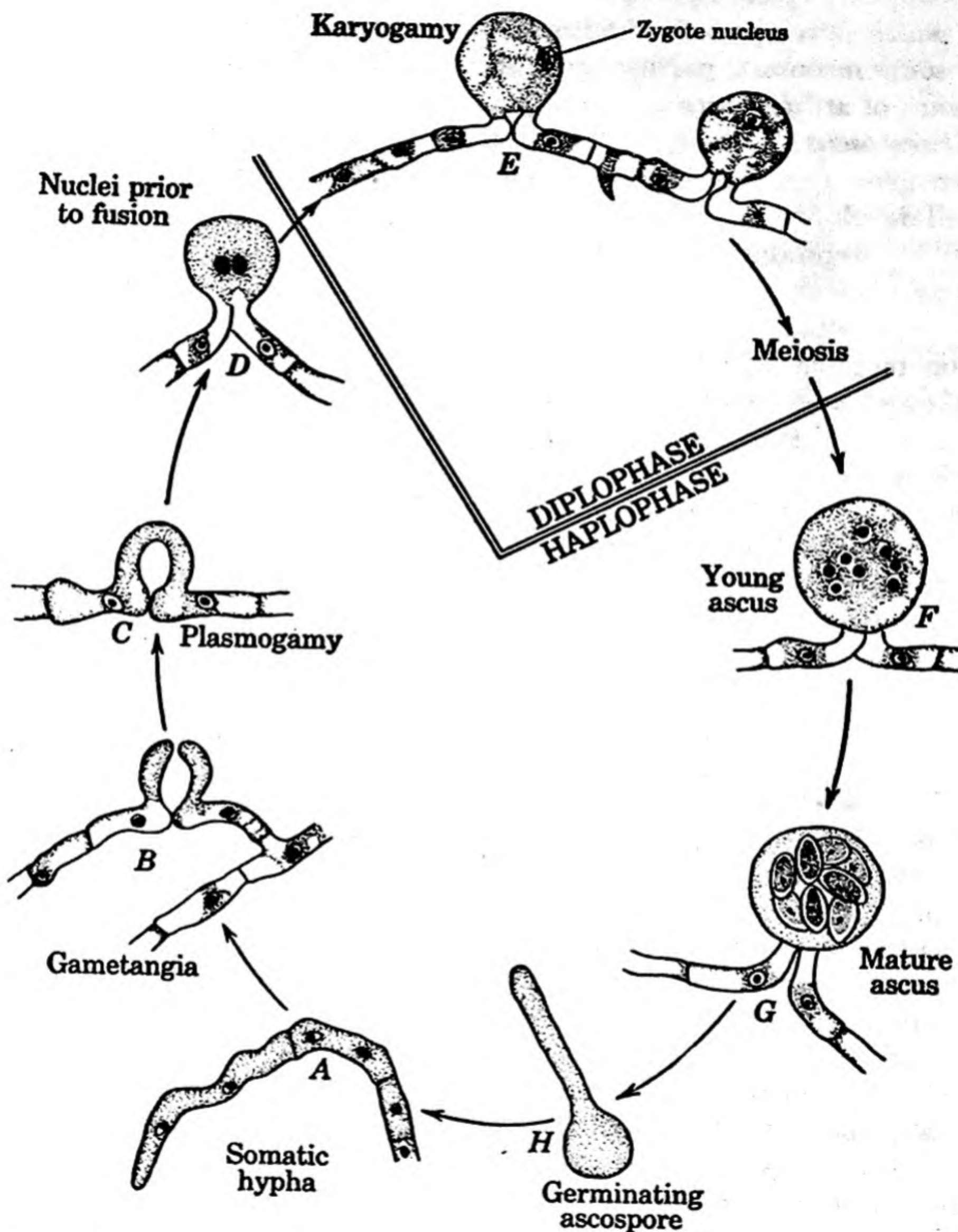


Figure 90. Life cycle of *Eremascus fertilis*. A–G, redrawn from Guilliermond, 1909, *Rev. gén. bot.*, 21:353–391, 401–419.

Occurrence, and Importance to Man. Yeasts are well distributed over the surface of the earth. They are particularly abundant in substrata which contain sugars, such as the nectar of flowers and the surface of fruits. They are also found in the soil, in animal excreta, in milk, on the vegetative parts of plants, and in other habitats.

Yeasts are noted particularly for their ability to ferment carbohydrates; hence the name *Saccharomycetes* (Gr. *saccharon* = sugar + *myketes* = fungi) is applied to them. Because of this property and the resultant alcohol and carbon dioxide, brewers and bakers employ yeasts in their industries. In the brewery the alcohol is the industrial product; in the bakery the carbon dioxide is the important product and the alcohol is waste. By selection and breeding, certain strains of yeasts have been developed which are industrially superior to the wild types. Wild yeasts, however, still play an important role in various fermentations, such as that of wine, and that of the cacao bean, to which they impart an aromatic flavor. The universal employment of yeast in baking and brewing has resulted in the establishment of another industry, the commercial preparation of yeast cake. By pressing into cubes great numbers of yeast cells together with inert matter such as starch, the compressed and dry yeast cakes of commerce, so useful in industry and in the home, are prepared. The high vitamin content of yeasts makes them particularly valuable as food.

The same properties which make yeasts useful also make them destructive so far as man is concerned. If a person is interested in making wine or other alcoholic drinks, he finds yeasts indispensable, but if he is manufacturing grape juice or sweet cider he must exclude them. Yeasts easily destroy soft cheeses of considerable moisture content and similar foods, for they impart an objectionable "yeasty" flavor.

Lipomyces neoformans is said to be the perfect stage of *Cryptococcus neoformans*, the cause of cryptococcosis, a serious human disease.¹ A number of asporogenous yeasts are also pathogenic to man, causing serious infection. We shall discuss these briefly in Chapter 18 under the Deuteromycetes.

Somatic Structures. In contrast to most other Ascomycetes the yeasts are unicellular organisms. They possess a definite cell wall which contains some chitin among other compounds, and a demonstrable but minute nucleus surrounded by cytoplasm. A large vacuole occupies a big portion of the yeast cell. Other inclusions are

¹ See page 409.

embedded in the cytoplasm. In spite of the fact that the cytology of the yeast cell has been investigated by a large number of competent investigators over many decades, the controversy over the structure of the nucleus and the identity of other inclusions continues undiminished (Winge and Roberts, 1958; Yuasa and Lindegren, 1959). One difference of opinion centers on whether the vacuole is a part of the cell nucleus or whether the two are separate entities. Electron microscope studies of ultra-thin sections of *Saccharomyces cerevisiae* (Agar and Douglas, 1957; Hashimoto *et al.*, 1958) and of *Schizosaccharomyces octosporus* (Conti and Naylor, 1959, 1960) show that the nucleus is surrounded by a membrane and is distinct from the vacuole. These studies further appear to show that the general structure of the yeast cell is comparable to that of other cells (Figure 91).

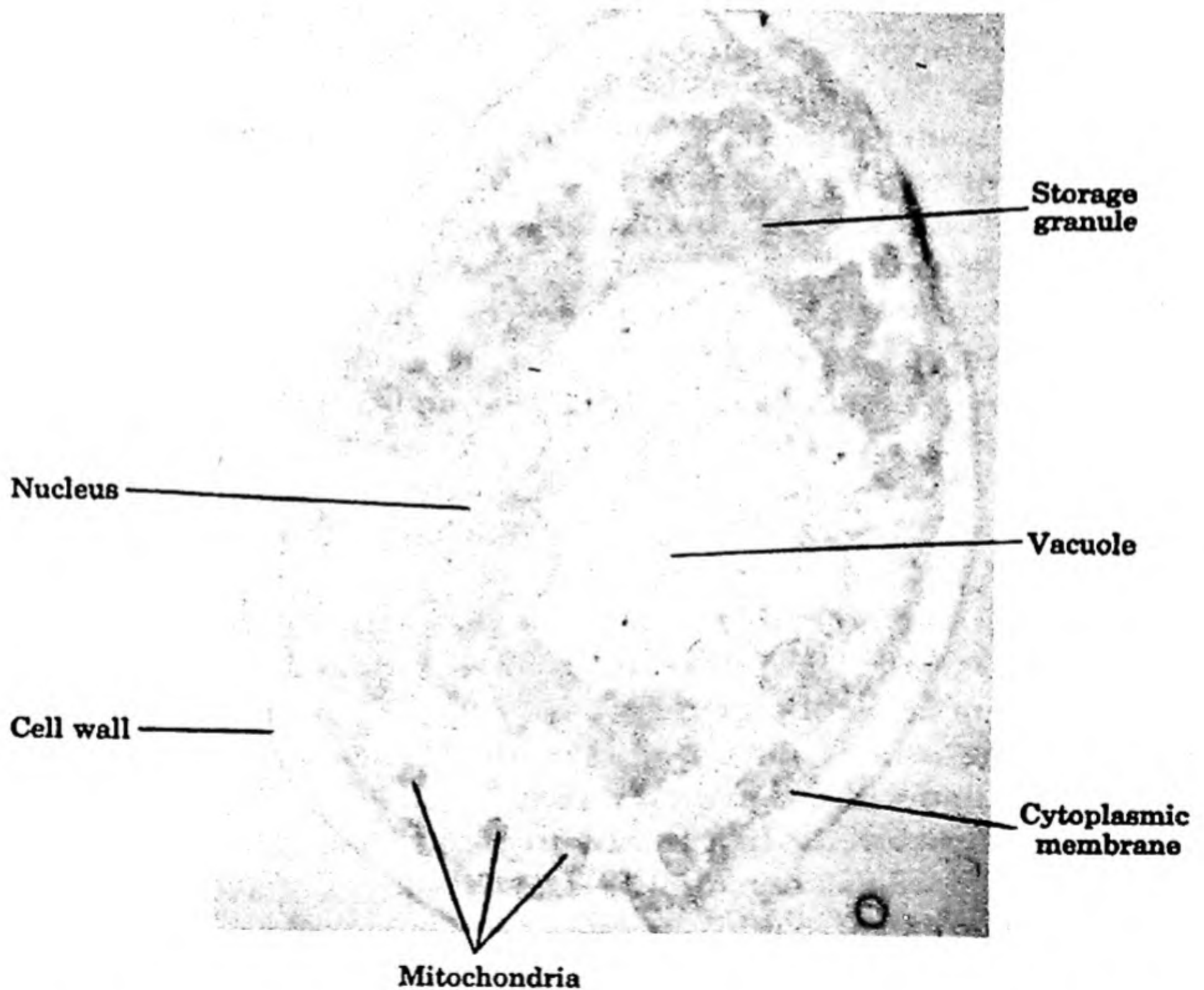


Figure 91. Electron micrograph of *Saccharomyces cerevisiae*. Courtesy Agar and Douglas, 1957, *Jr. Bact.*, 73:365-375.

Yeast cells vary in shape with the species and even within the species. They may be globose, ovoid, elongated, or rectangular in shape. They sometimes adhere in chains, forming a pseudomycelium (Figure 92).

Individually yeast cells appear colorless, but when grown on artificial solid media they produce colonies which may be white, cream colored, or tinged with brownish pigments. The colonies of some of the imperfect yeasts are brilliantly colored. Colony characteristics are useful in the taxonomy of yeasts, a very difficult group to classify. Physiological characteristics also are used to a great extent in determining yeast species.

Asexual Reproduction. We usually group yeasts into the budding yeasts and the so-called fission yeasts, depending on their type of asexual reproduction. We apply the name budding yeasts to those which commonly reproduce by budding. In this process the protoplasm of the cell, covered by a thin membrane, pushes out of the cell wall in the form of a bud and forms a daughter cell. The bud enlarges until it is separated from the mother cell by a constriction at the base. The daughter cell may, in turn, produce a bud while still attached to the parent cell. A chain of cells may thus be formed. Such chains may branch if more than one bud are produced from any one yeast cell in the chain, as sometimes happens. During the process of budding, the nucleus divides, one daughter nucleus passing into the bud, the other remaining in the mother cell. Most known yeasts reproduce by budding. In the common bread yeast, *Saccharomyces cerevisiae*, the nuclear membrane persists throughout nuclear division, and the electron microscope reveals no evidence of chromosome formation (Hashimoto *et al.*, 1959). However, it is well known that presently available techniques are inadequate for the study of chromatin behavior by electron microscopy, and conclusions based on such studies alone are apt to be misleading.

The fission yeasts reproduce by transverse division. The parent cell elongates, the nucleus divides, and a transverse wall (septum) is laid down somewhere near the middle, separating the mother cell

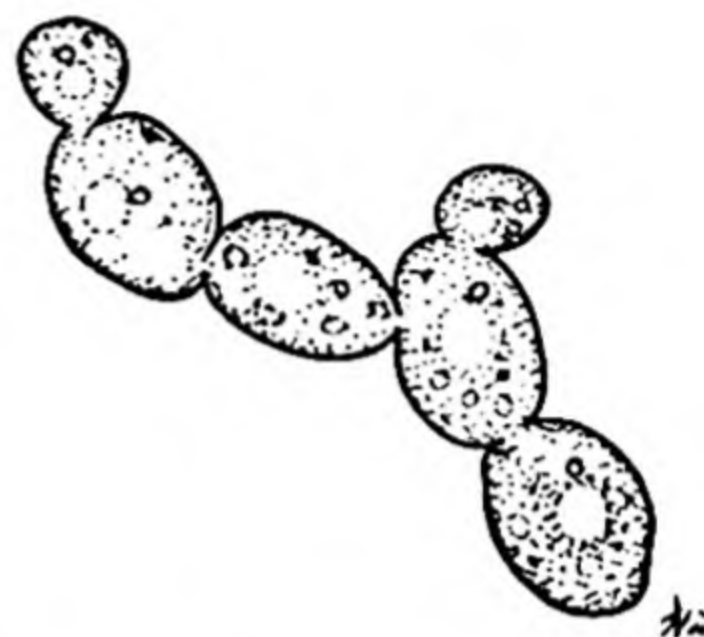


Figure 92. Chain of yeast cells (pseudomycelium) produced by budding.

into two uninucleate daughter cells. This septum is formed by annular growth beginning at the wall and proceeding inward. The new wall thickens before the daughter cells separate (Conti and Naylor, 1959).

Some yeasts combine these two methods. A bud is formed in the usual way from the mother cell, but, instead of a constriction taking place, a septum is laid down which separates the bud from the mother cell.

Sexual Reproduction. Sexual union in the yeasts takes place either between two somatic cells or between two ascospores which assume the function of copulating gametangia, unite, and form a zygote cell. Eventually an ascus forms which contains ascospores, their number depending on the number of nuclear divisions which take place and on the subsequent development of the nuclei. Four or eight ascospores per ascus is the usual number, but other numbers also may be encountered.

In the heterothallic *Hansenula wingei*, Wickerham (1956) has shown that opposite mating types will agglutinate when brought together in culture. Agglutination greatly increases zygote formation but not ascospore formation. The zygotes produce large numbers of diploid cells, only a few of which ever form ascospores. The most probable explanation of this phenomenon, according to Brock (1958a, b; 1959a, b), is that agglutination is due to a specific substance (probably a protein) present on the wall of one of the mating types which combines with a specific substance (probably a polysaccharide) present on the wall of the opposite mating type.

How widespread the phenomenon of sexual agglutination is we do not as yet know. Wickerham (1958) reported this mechanism in four genera and stated that it appears to be frequent among yeasts (Figure 93). Brock (1959b), on the contrary, stated that most other heterothallic yeasts do not employ this mechanism.

The ascospores formed by the yeasts are often globose or ovoid, as in *Debaryomyces*, *Saccharomyces*, *Schizosaccharomyces*, and *Saccharomycodes* (Figure 94A). Other yeasts form different types of ascospores. Thus, in *Pichia* and some species of *Hansenula* the ascospores are hat-shaped; in other species of *Hansenula* they may be hemispherical or shaped like the planet Saturn (Figures 94B, C). Generally the ascus breaks open and thus releases the ascospores which, by means of asexual methods of reproduction—budding or fission—give rise to somatic cells typical of the species.

Life Cycle. According to Guilliermond (1940), yeasts exhibit three life cycle patterns. In the first of these, exemplified by *Schizo-*

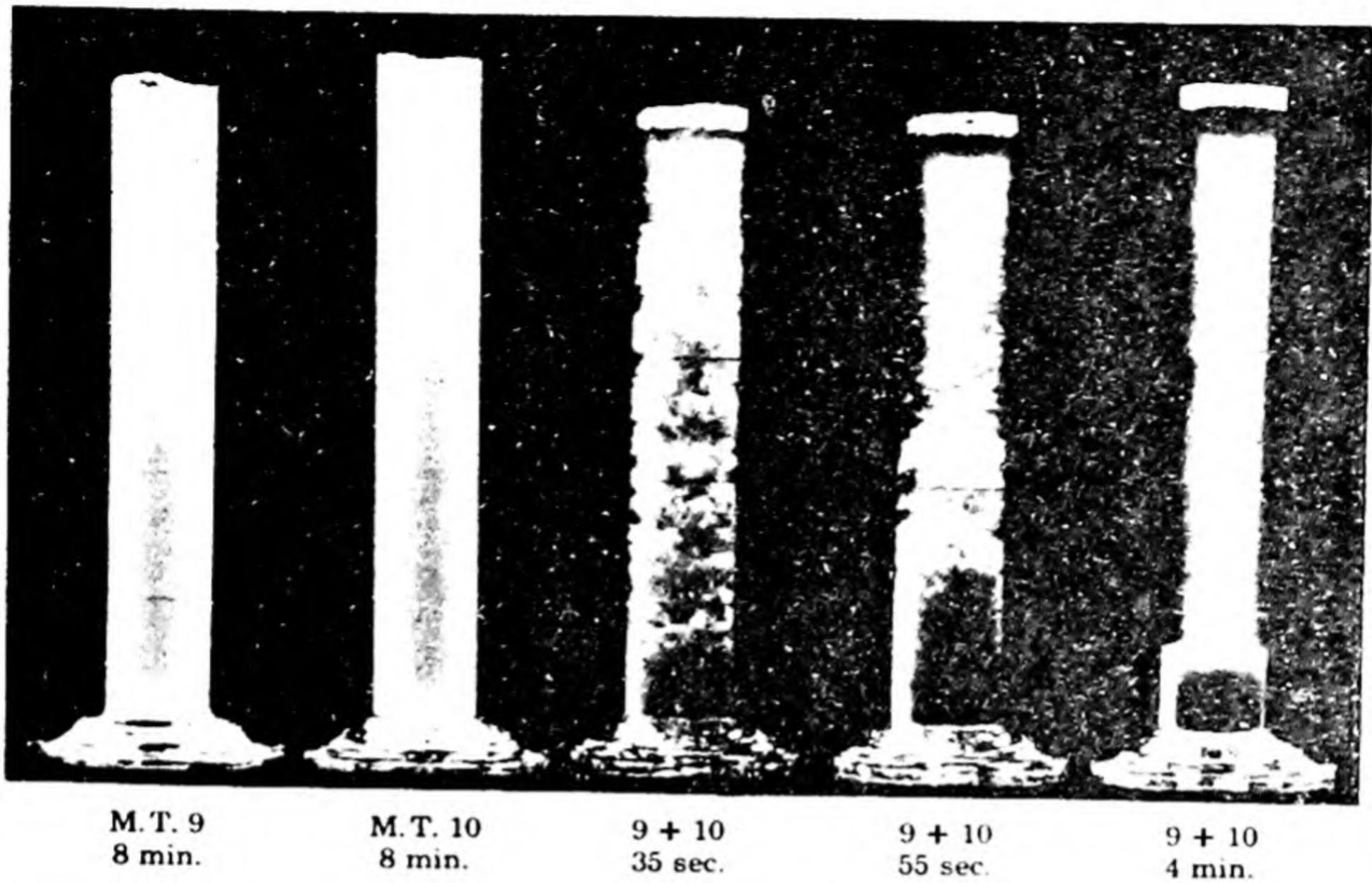


Figure 93. Mutual agglutination of opposite mating types (M.T. 9 and 10) of *Hansenula matritensis*. Courtesy L. J. Wickerham.

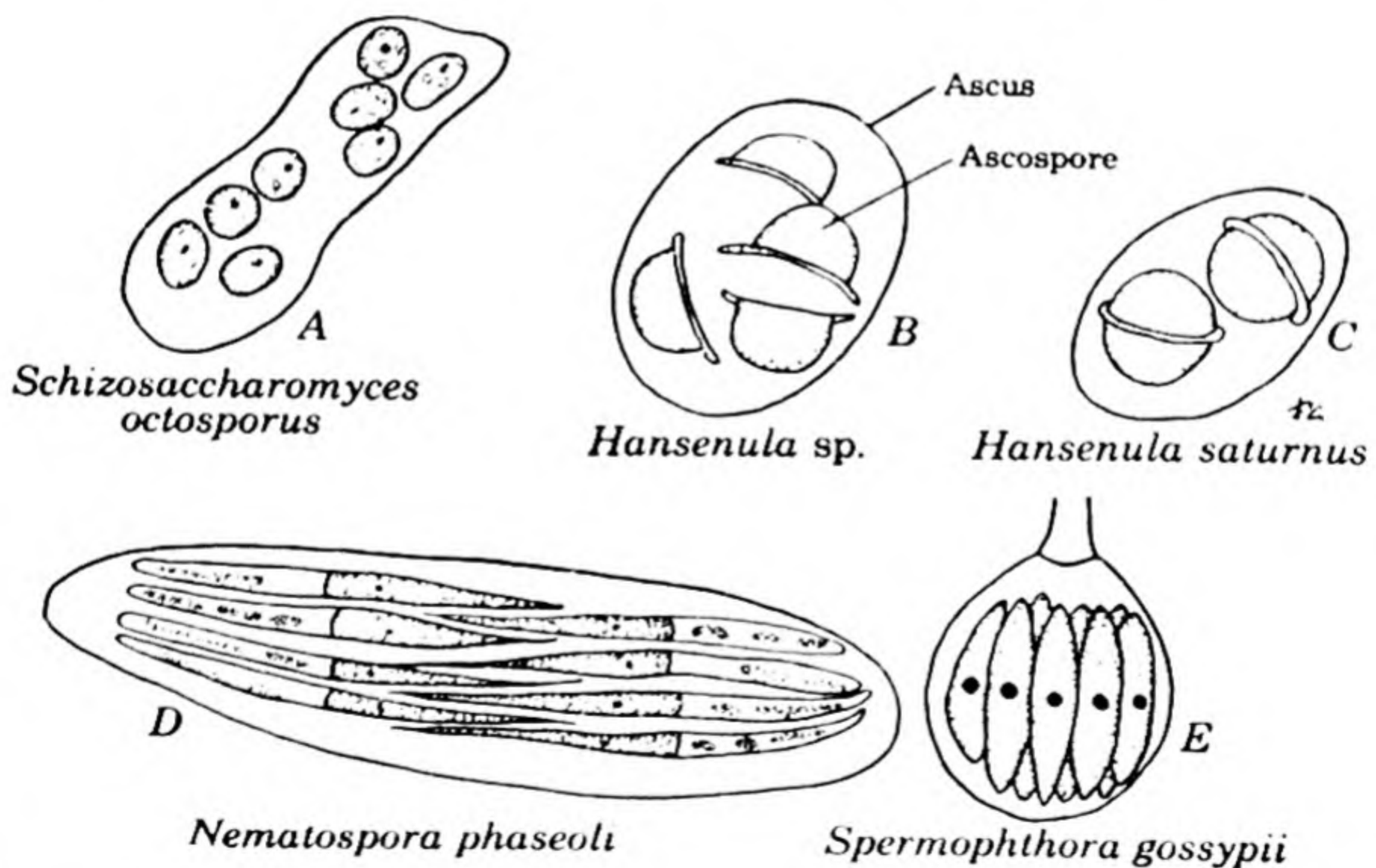
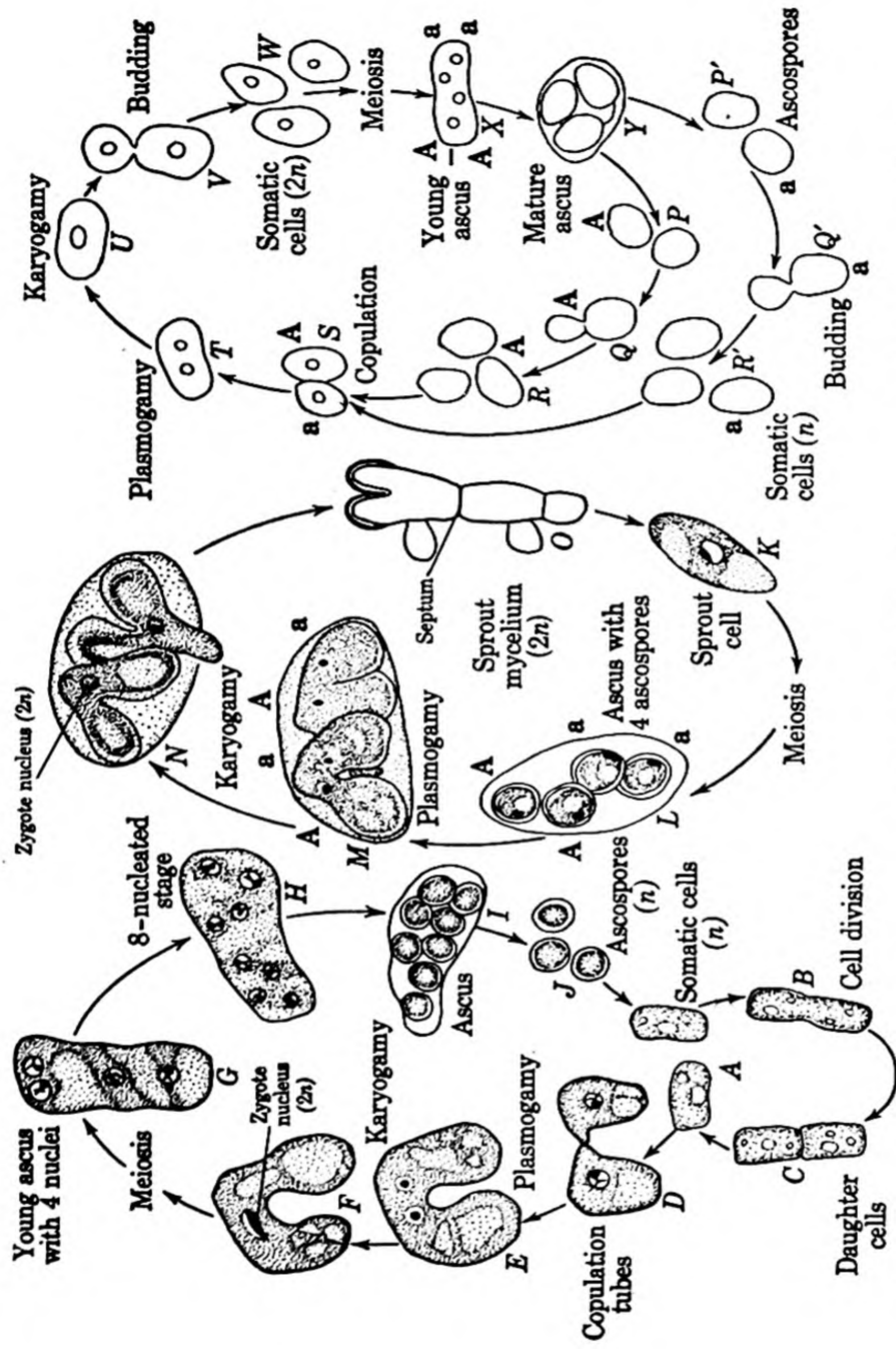


Figure 94. Various types of yeast ascospores. D, redrawn from Wingard, 1925, *Bull. Torrey Bot. Club*, 52:249-290; E, redrawn from Guillermond, 1928, *Rev. gén. bot.*, 40:328-342, 397-414, 474-485, 555-574, 606-624, 690-704.

saccharomyces octosporus (Figures 95A–J), the diploid stage is very short, being confined to the zygote cell, which undergoes meiosis immediately after karyogamy and develops the ascospores. The life cycle of this well-known homothallic organism is as follows. The somatic cells are elongated, uninucleate, and haploid. Transverse division takes place in each cell, dividing it into two daughter cells which separate, elongate, mature, and divide again. Any cell is apparently a potential gametangium. In sexual reproduction, two cells come in contact. The walls dissolve at the point of contact, and the nuclei move into the narrow canal which has been formed. The nuclei now approach each other and fuse, with their membranes dissolving at the site of fusion but remaining intact elsewhere (Conti and Naylor, 1960). The cytoplasm flows into the canal which now widens considerably, and the two cells have united. The fusion nucleus now undergoes three divisions, the first two of which constitute meiosis, and within the zygote cell, which is now the ascus, eight ascospores are formed, one around each nucleus. The breaking of the ascus wall finally liberates the ascospores, each of which now behaves like a somatic cell, giving rise to daughter cells by transverse division. Widra and DeLamater (1955) report that mitosis and meiosis in this species follow the classic pattern, and that the haploid number of chromosomes is four.

The second life cycle pattern in yeasts, of which *Saccharomyces ludwigii* (Figures 95K–O) is an example, features a long diploid somatic stage and a very short haploid phase. In this species it is the ascospores which copulate. Two adjacent ascospores of opposite mating types A and a fuse (plasmogamy and karyogamy) within the ascus and form a diploid cell. This germinates by a germ tube which pushes through the ascus wall and acts as a sprout mycelium from which the yeast cells are budded. These buds are separated from the mother cells by septa and soon become severed. Meiosis converts these somatic, diploid yeast cells into asci, each producing four haploid ascospores, two of each mating type. Thus, the ascospores represent the only haploid phase of the life cycle.

In the third life cycle pattern, exemplified by *Saccharomyces cerevisiae*, the yeast of commerce, both haplophase and diplophase are perpetuated by budding so that both phases are of equal importance and may be said to constitute something of an alternation of generations. Copulation takes place between haploid cells and forms a diploid cell (Figures 95S–U). Such a cell multiplies by budding, producing a large number of diploid cells which are large and vigorous (Figures 95V, W). Eventually, the diploid cells become con-



Schizosaccharomyces octosporus

Saccharomyces ludwigii

Saccharomyces cerevisiae

Figure 95. Comparative life cycles of three types of yeasts. D-G, K-N, redrawn from Guilliermond, 1905, *Rev. gén. bot.*, 17:338-376; H, constructed; O, redrawn from Guilliermond, 1905, *Bull. soc. mycol. France*, 19:19-32; P-Y, diagrammatic.

verted into asci, each one containing four haploid ascospores (Figures 95X, Y). After the ascospores are set free from the ascus they begin budding, each forming a population of haploid cells (Figures 95P-R'). These are smaller than the diploid cells. The Lindegrens (1943) have shown that in this organism the ascus derived from an Aa zygote cell produces four ascospores, two of which are of one strain A and the other two of the other strain a.

Although correct as far as it goes, the life cycle given above and in Figure 95 does not convey the entire picture, for a great many variations have been discovered. One of the most interesting is the fusion of two cells of the same mating type in the presence of a diploidization gene D. This results in stable diploid cultures which eventually form typical four-spored asci (Winge and Roberts, 1958).

A discussion of yeast life cycles, no matter how short, should not neglect to mention *Kluyveromyces polysporus*, discovered in 1956 by van der Walt in South Africa. This species appears to meet all the requirements of a yeast, but produces a multispore ascus. *Kluyveromyces polysporus* is a homothallic budding yeast in which the zygote is the only diploid stage. Meiosis of the zygote nucleus is followed by a series of mitotic divisions which eventually result in a multispored ascus. However, some asci begin to bud just after meiosis has occurred, giving rise to uninucleate, haploid cells (Roberts and van der Walt, 1959).

family SPERMOPHTHORACEAE

The Spermophthoraceae are all plant parasites. Our knowledge concerning them comes chiefly from the studies of Guilliermond (1928, 1936). Gäumann (1952) brings together four genera in this family: *Spermophthora*, *Eremothecium*, *Ashbya*, and *Nematospora* (Figure 94D).

In *Spermophthora*, the spindle-shaped ascospores (Figure 94E) germinate and produce aseptate, coenocytic hyphae which give rise to large intercalary, sac-like structures delimited by septa from the parent hyphae. The nuclei in these structures divide until about forty nuclei have been formed. Uninucleate spore-like bodies are then produced which, upon release, behave either as spores, germinating and forming mycelium, or as gametes, copulating in pairs and forming zygotes. The zygote, upon germination, gives rise to a short, diploid, branched mycelium which produces single, round asci at the tips of the branches. Each ascus contains eight haploid ascospores.

order TAPHRINALES

The fungi which we classify in the Taphrinales are all parasitic on vascular plants, causing malformations of the tissues they attack and producing such disease symptoms as leaf curl, puckering, pockets, blisters, and witches' broom. *Taphrina deformans*, the cause of peach leaf curl, is the best-known species in this order. Peach leaf curl, a disease which occurs wherever peaches are grown, still does considerable damage, but is one which we have learned to control. Some other economically important species are *Taphrina pruni*, which causes plum pockets; *Taphrina cerasi*, which causes witches' broom of cherries; and *Taphrina coerulescens*, which causes a curling and puckering of oak leaves.

The Taphrinales resemble the yeasts in that the ascospores, like yeast cells, multiply by budding. On artificial media no mycelium is formed; the yeast stage, which is the only one produced, forms a typical yeast colony. Guilliermond (1940) believed that the yeasts of the second life cycle type (short haplophase and prolonged diplophase) have been derived from the Taphrinales.

The Taphrinales differ from the yeasts in that in nature they produce a definite, true mycelium; they differ from the other Endomycetales in that the ascus is not produced directly from a zygote cell resulting from the copulation of two cells, but rather from a special, binucleate, ascogenous cell derived from the mycelium and resembling, in its method of formation, a chlamydospore.

Classification. The Taphrinales include a single family, the Taphrinaceae, and, according to most authors, a single genus, *Taphrina*. Some authors, however (Kramer, 1958), also place the Protomycetaceae in this order.

Somatic Structures. The mycelium of *Taphrina* is composed of septate hyphae, consisting of typically binucleate cells. These hyphae may be intercellular or subcuticular, or may grow within the walls of the epidermal cells. Intercellular hyphae may penetrate rather deeply into the host tissues. Kramer (1960/1961) has made a detailed study of the hyphae of several species with intercellular and subcuticular mycelium. His article should be consulted for the details.

Asexual Reproduction. Asexual reproduction is by small, ovoid or spherical, uninucleate, haploid, yeast-like blastospores which bud directly from the ascospores while the latter are still within the ascus, or after they have been released. The blastospores either may

bud and produce more blastospores or may germinate and form mycelium which infects the host.

Sexual Reproduction. The Taphrinales produce no sex organs whatever. In this respect they resemble the yeasts. The copulation of conidia which originate from ascospores by budding has been reported for *Taphrina epiphylla* and *Taphrina klebahnii*. In *Taphrina deformans*, however, Miss Ella Martin (1940) showed that no plasmogamy takes place, and that karyogamy occurs between sister nuclei, as I shall explain in the description of the life history of this organism. Kramer (1960/1961) states that “. . . it is generally accepted that the dicaryotic condition . . . which has been found to be present in all species studied, arises through a mitotic division of the ascospore or blastospore nucleus at the time of germination.”¹

Life Cycle. Several workers have investigated the life cycle of *Taphrina deformans* and have reported somewhat contradictory results. I am basing the following short account on Miss Ella Martin's paper (1940), from which I have also taken some drawings and arranged them in the life cycle diagram in Figure 96.

The ascospores, soon after they are formed, produce small, round or ovoid blastospores by budding (Figure 96A). This often takes place within the asci and continues after the spores have been released to the outside. The blastospores, like the ascospores, are uninucleate and haploid. On the surface of the host, the blastospores may continue to bud, producing secondary blastospores (Figure 96B), or may germinate by germ tubes which infect the host and produce the mycelium (Figure 96C). At the time of germination, the conidial nucleus divides, and the resulting pair of nuclei migrate into the germ tube. As the hypha grows, conjugate division of the nuclei perpetuates the binucleate condition of the hyphal cells (Figure 96D).

The mycelium grows and branches, spreading between the cells and penetrating the various tissues of the host. Hyphal strands eventually become more or less massed in the subcuticular region, and here break up into their component binucleate cells. These cells are ascogenous cells (Figure 96D) which are often called chlamydospores because of their method of formation. Karyogamy occurs within each ascogenous cell, and about this time the cell begins to elongate (Figure 96E). While this elongation is proceeding, the diploid nucleus divides mitotically, and one daughter nucleus remains near the base of the cell while the other moves toward the growing

¹ Quoted by permission of *Mycologia*.

tip (Figure 96F). A septum then develops between these two nuclei, separating the cell into a basal stalk cell and an upper ascus mother cell (Figure 96G). The protoplast of the basal cell soon disintegrates, leaving the cell empty, while the upper cell is being converted into an ascus. Meiosis and a subsequent mitotic division re-

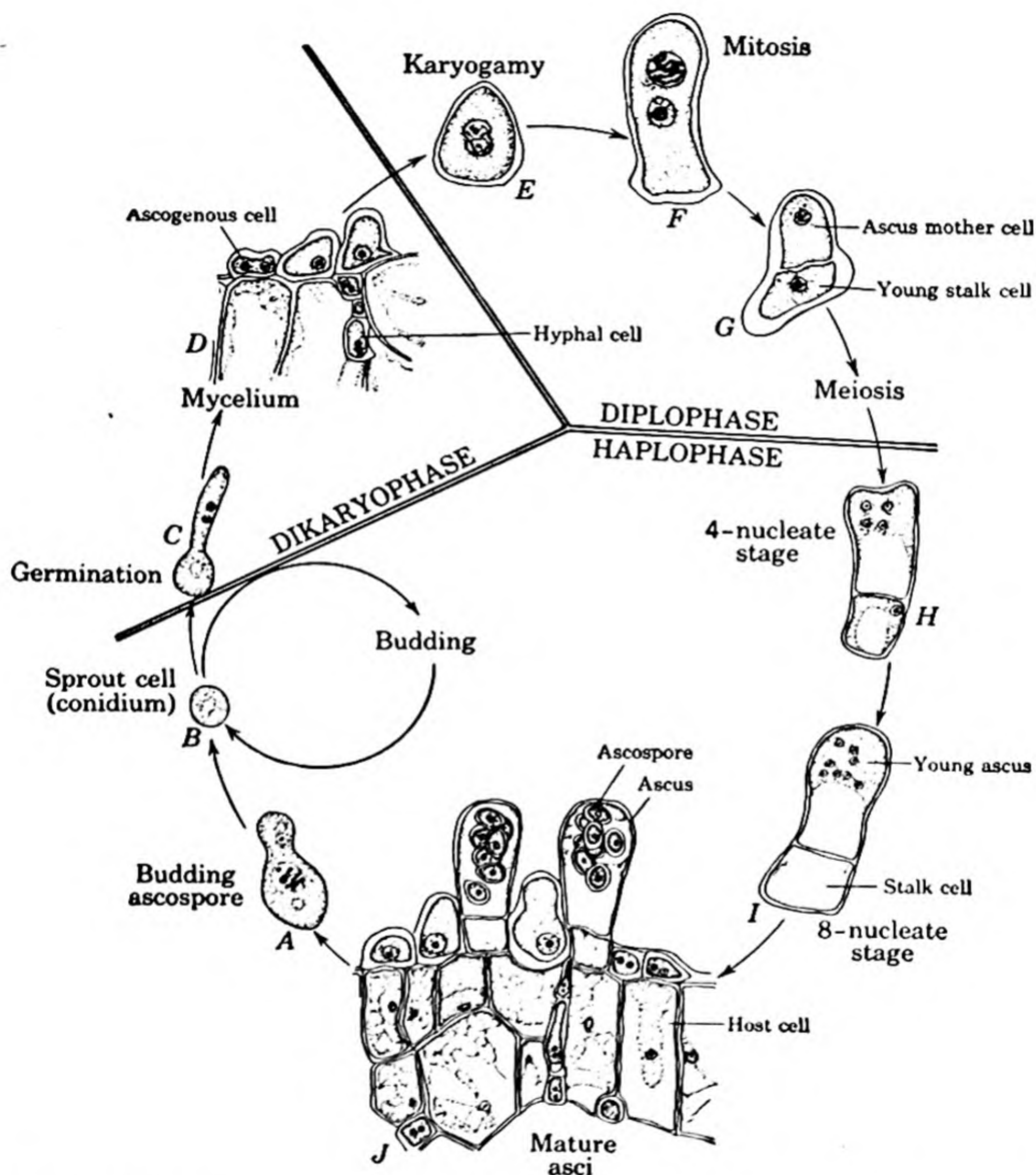


Figure 96. Life cycle of *Taphrina deformans*. Redrawn from Miss Martin, 1940, *Am. Jr. Bot.*, 27:743-751.

sult in the formation of eight nuclei (Figures 96H, I). Each nucleus, with an adjacent portion of cytoplasm, is encompassed by a wall and develops into an ascospore (Figure 96J).

As the ascus mother cells enlarge, they exert pressure on the host cuticle from below, and eventually break through to form a compact, surface layer of asci—the hymenium—on the epidermis of the host. No fruiting structure of any sort is formed; the asci remain naked and release the ascospores into the air. After the ascospores are released, they begin to bud and form numerous blastospores. These eventually produce germ tubes which infect the host. In most species ascospore budding also takes place within the ascus.

The phylogeny of the Hemiascomycetidae is a matter of speculation. Guilliermond believed that the mycelioid forms have given rise to the yeast forms by reduction, the yeasts of the *Saccharomyces* type having been derived from the Taphrinales. Although many mycologists consider the yeasts and yeast-like fungi primitive groups, others, thinking of them as the highest stage in the evolution of the Ascomycetes, consider them reduced, degenerate forms.

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13 sub-class
EUASCOMYCETIDAE
series
PLECTOMYCETES
black molds, blue molds

Introduction. The Euascomycetidae constitute a large sub-class of Ascomycetes in which the asci are usually unitunicate. The asci typically develop from ascogenous hyphae and, in the majority of species, are enclosed in a true ascocarp—cleistothecium, perithecium, or apothecium—which may or may not be associated with a stroma. Some species, however, form their asci directly within locules in stromata in a manner characteristic of the sub-class Loculoascomycetidae (Chapter 17). In a few others the “ascocarp” is nothing more than a loose, cottony mass of hyphae which surrounds the sex organs and, eventually, the asci. Typically, the Euascomycetidae develop functional sex organs, but sexual degeneration, especially of the male gametangium, has been demonstrated in a number of species and appears to be the trend, at least in some groups.

Life History Pattern. The life history of the Euascomycetidae, in its gross aspects, follows a more or less typical pattern from which, however, individual fungi may deviate considerably. The general pattern may be described as follows. When the ascospores mature, they are eventually released from the asci and ascocarps and are disseminated; under favorable conditions they germinate, each producing a germ tube which grows into the mycelium. The mycelium now bears the conidiophores, which produce great numbers of conidia. The latter perpetuate the fungus by producing more mycelium. The conidial cycle is generally repeated many times during the growing season. When conditions favoring sexual reproduction prevail, the mycelium forms fruiting bodies in which asci and ascospores develop

in the manner already described in Chapter 11. The Euascomycetidae go through the winter in the mycelial, ascocarp, or conidial stage, depending on the fungus, the substratum, and the environment, but, in general, the mycelial or ascocarp stages are the ones which overwinter (Figure 97).

Classification. Because mycologists as yet lack knowledge of the morphology and cytology of most Ascomycetes, they have had to speculate considerably about the relationships between members of this group. Consequently, they have not stabilized their taxonomic views, and the number of orders and families which different systematists recognize varies. Among the criteria which have been used to separate different groups are the type of ascocarp, the nature of the ascocarp wall, the color of the ascocarp, the nature of the substratum, the position of the ascocarp with reference to the substratum, the type of ascus, the position of asci in the ascocarp, the method of ascus opening, and the presence of paraphyses or other sterile threads. Some of these criteria have stood the tests of time and of newer research; others have been abandoned by modern systematists.

The modern era in the taxonomy of the ascocarpic Ascomycetes begins with a paper published in 1932 by Professor J. A. Nannfeldt of the Botanical Institute of the University of Uppsala in Sweden. Nannfeldt recognized three major groups: the Plectascales with cleistothecia, the Ascohymeniales with perithecia or apothecia, and the Ascoloculares with ascostromata. Since then, contributions from many laboratories have resulted in various modifications of Nannfeldt's system which different authors have developed and adopted. In the United States, the University of Georgia has been pre-eminent in its contribution to our knowledge of the Ascomycetes, with Professors Julian Miller and E. S. Luttrell developing a system of classification which emphasizes the structure of the ascus and the ascocarp centrum. The system which we shall adopt in this book is based chiefly on Luttrell's discussions as set forth in 1951 and 1955, and as adopted to a large extent by Martin (1961).

The sub-class Euascomycetidae may be conveniently subdivided into four series which are at least as well defined as most taxonomic categories. These are the Plectomycetes, the Pyrenomycetes, the Discomycetes, and the Laboulbeniomycetes. These may be characterized as follows.

The *Plectomycetes* produce their asci at various levels. The asci are typically globose or broadly oval and evanescent; *i.e.*, they deliquesce and release the spores. The ascocarp is usually, but not necessarily, a completely closed cleistothecium.

The *Pyrenomycetes* produce their usually club-shaped or cylindrical asci in a layer (hymenium) which lines the base and often the sides of the inner wall of a perithecium, or in basal tufts. The asci are usually persistent. The perithecium may or may not be

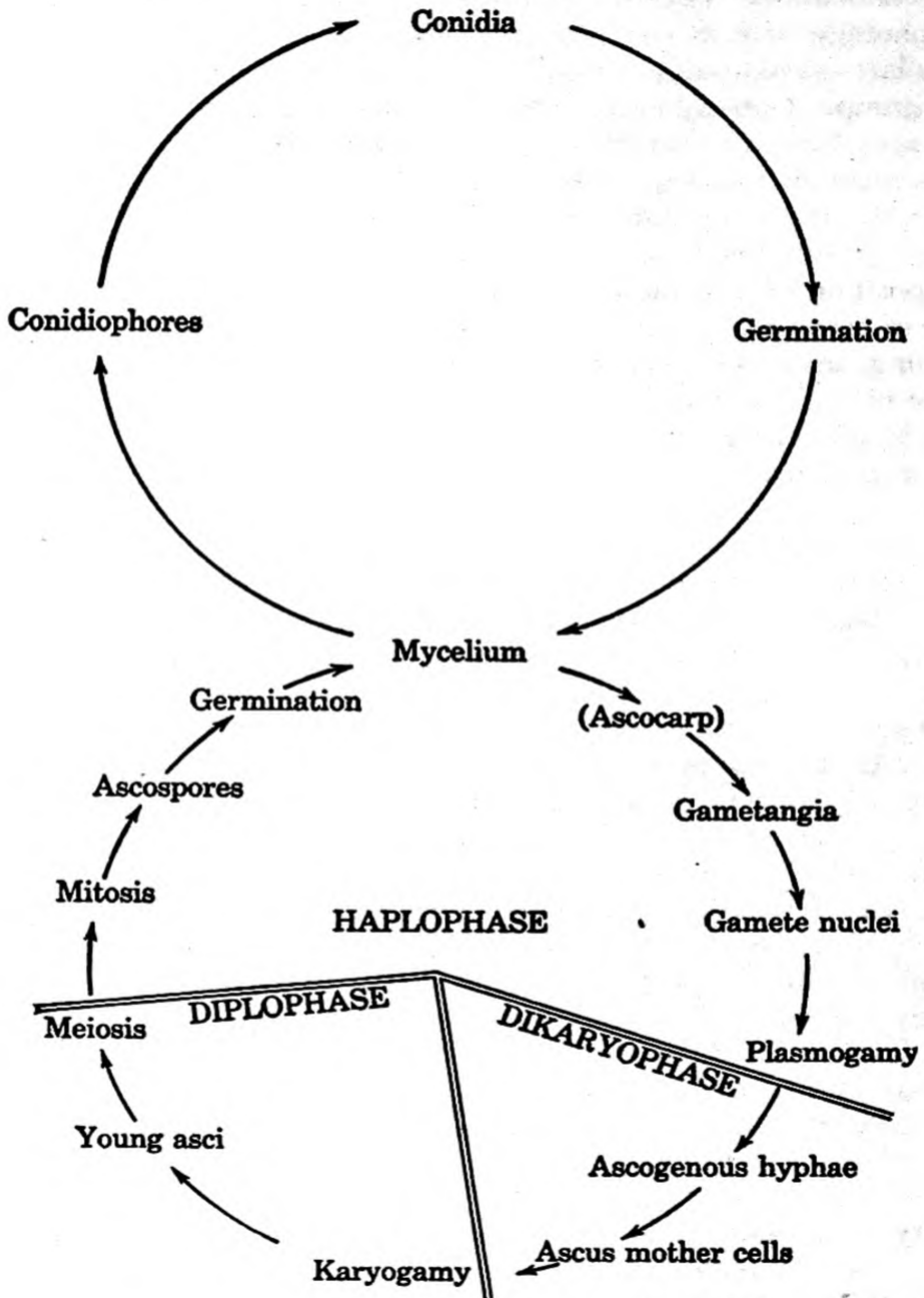


Figure 97. Life cycle pattern of the Euascomycetidae.

embedded in a stroma, but in either situation it has a definite peripheral wall of its own.

The foregoing is a restricted definition of the Pyrenomycetes. As most mycologists use this term, the group includes not only the true perithecial fungi but also those with ascostromata. In its wider sense, therefore, the term Pyrenomycetes encompasses the Loculoascomycetidae as well.

The *Discomycetes* are those fungi which bear their club-shaped or cylindric asci arranged in a hymenium in an open ascocarp (apothecium). In the truffles (order Tuberales) the ascocarps are produced and mature below the ground, and in most species remain closed.

The *Laboulbeniomyces* are highly specialized, superficial parasites on insects whose thallus consists of an anchoring foot supporting a few cells or filaments or a somewhat more extensive mycelium. A cluster of broadly club-shaped asci is developed in a perithecium-like ascocarp. The asci deliquesce.

Most authors find these groupings convenient, but have not given them formal rank in the classification system. It is not possible as yet to know whether they represent true lines of evolutionary development. At present they should be regarded only as convenient groupings of Ascomycetes which show similarities in certain structural characteristics.

Most of the orders included in the key below are those recognized by Martin (1961). The limits of these orders, the concepts on which they are defined, and their groupings into series vary greatly. For other classification systems of the Ascomycetes consult Bessey (1950), Gäumann (1952), Luttrell (1951), Miller (1949), Moreau (1952-1953), Nannfeldt (1932), Wolf and Wolf (1947), and Chadeaud (1960).

SIMPLIFIED KEY TO THE ORDERS OF THE SUB-CLASS EUASCOMYCETIDAE

(Modified from G. W. Martin, 1961)

- | | |
|--|--------------------------------|
| A. Saprobes or parasites of plants or animals; mycelium abundant, well developed | |
| B. Asci scattered within the ascocarp or united in spore balls within a spore-cyst; evanescent | Series
<i>Plectomycetes</i> |
| C. Ascocarps sessile | |
| D. Ascocarps without ostioles | <i>Eurotiales</i> |
| DD. Ascocarps ostiolate | <i>Microascales</i> |
| CC. Ascocarps stalked | <i>Onygenales</i> |

BB. Asci in a basal or peripheral layer, forming a hymenium, or in basal tufts; typically persistent, sometimes evanescent

E. Ascocarp closed; mostly ostiolate

Series
*Pyrenomyces*¹

F. Ascocarp with perithecial wall of its own

G. Mycelium largely superficial

H. Mycelium white; asci in cleistothecia

Erysiphales

HH. Mycelium dark; ascocarps ostiolate

Meliolales

GG. Mycelium within the substratum

I. Asci evanescent

Chaetomiales

II. Asci persistent

J. Ascospores thread-like

Clavicipitales

JJ. Ascospores not thread-like, sometimes needle-shaped

K. Ascocarps and stromata, if present, dark, membranous or carbonous

L. Ascal bases not gelatinizing; mature asci remaining attached to the inner perithecial wall

Sphaeriales

LL. Ascal bases gelatinizing; mature asci loose in the perithecial cavity and exuding through the ostiole

Diaporthales

KK. Ascocarps and stromata, if present, brightly colored, soft, fleshy, or waxy

Hypocreales

FF. Asci in ascostromata

M. Ascocarp ostiolate; ostiole funnel-shaped

Coryneliales

MM. Ascocarp opening irregularly or by an ostiole, but ostiole not funnel-shaped

Coronophorales

EE. Ascocarp an open apothecium or a modified form thereof

Series
Discomycetes

¹ See page 265 for a wider use of this term.

N. Ascocarps above ground	
O. Asci inoperculate	
P. Ascospores thread-like	<i>Ostropales</i>
PP. Ascospores not thread-like, sometimes needle-shaped	<i>Helotiales</i>
OO. Asci operculate or suboperculate	<i>Pezizales</i>
NN. Ascocarps below the ground	<i>Tuberales</i>
AA. Specialized exoparasites of insects or arachnids; thallus usually limited, sometimes consisting of but a few cells	Series <i>Laboulbeniomycetes</i> <i>Laboulbeniales</i>

series PLECTOMYCETES

The fungi we group in the series Plectomycetes have several characteristics in common which seem to separate them from other Euascomycetidae, but the distinction is not absolute because of the ever-present intermediate forms. The asci are globose or broadly club-shaped; they arise at different levels in the ascocarp and are, therefore, irregularly arranged; they have no natural opening, but release the ascospores by deliquescing and setting them free in the ascocarp. The ascocarp either is completely closed (cleistothecium) or has an ostiole. In one small group, the asci are united in spore balls within a spore cyst. As treated here, the Plectomycetes include three orders: the Eurotiales, the Onygenales, and the Microascales.

order EUROTIALES¹

With very few exceptions, the Eurotiales (also called Aspergillales² and Plectascales³) produce their cleistothecia on the mycelium without the formation of a stroma. The asci are formed from ascogenous hyphae of various lengths and are consequently scattered at various levels within the ascocarp. There is, therefore, no definite hymenial layer. The irregular distribution of the asci possibly represents the primitive condition, as opposed to a definite hymenial layer found in most Euascomycetidae.⁴

The order includes several hundred species of fungi, most of which are saprobes, but some of which are parasitic on plants, animals, and

¹ For an evaluation of the characters used to delimit this order see Cain (1956a).

² Bessey (1950).

³ Gäumann (1952).

⁴ But see Bessey (1950) for the view that the Eurotiales represent a more advanced condition.

human beings. The conidial stages of many of these fungi are of very common occurrence and are familiar to everyone under the names of black mold, green mold, and blue mold.

Depending on his point of view, the modern systematist classifies these fungi into from two (Martin, 1961) to seven (Bessey, 1950) families. We shall recognize three families, as follows:

SIMPLE KEY TO THE FAMILIES OF THE ORDER EUROTIALES

- | | |
|--|-----------------------|
| A. Asci in spore balls | <i>Ascospaeraceae</i> |
| AA. Asci not in spore balls | |
| B. Peridium, when present, a lax network of hyphae | <i>Gymnoascaceae</i> |
| BB. Peridium of closely interwoven hyphae usually forming a pseudoparenchyma | <i>Eurotiaceae</i> |

family ASCOSPHERACEAE

The *Ascospaeraceae*, a newly organized family, includes the beehive fungi *Ascospaera apis* and *Ascospaera alvei* (Spiltoir and Olive, 1955). These were formerly known as *Pericystis apis* and *alvei*, respectively, and were included by many mycologists in the Protomycetales. Spiltoir (1955) in a study of the life cycle of *Ascospaera apis* showed that this fungus has its affinities with the Eurotiales.

The *Ascospaeraceae* produce their asci from croziers. The asci, which are probably eight-spored, are united, in groups of several to many, into compact spore balls, which are produced in a sporangium-like structure called a spore cyst (Figure 98).

Ascospaera apis (and probably *Ascospaera alvei*) is dioecious (morphologically heterothallic), requiring two individuals for sexual reproduction. When two compatible individuals are brought together, one (the female) develops ascogonia with trichogynes. The "male" individual produces no sex organs, the sexual function being taken over by the somatic hyphae. Plasmogamy occurs when a trichogyne grows toward and contacts a "male" hypha. The main body of the ascogonium just below the trichogyne is an inflated **nutriocyte** (L. *nutrio* = to nourish + Gr. *kystis* = bladder) which receives the content of the trichogyne after plasmogamy has occurred. This protoplast now becomes covered with a wall and is the primary ascogenous hypha, which becomes septate, proliferates, and forms an ascogenous system within the nutriocyte. Certain binucleate cells form croziers in the usual way, and asci are produced in compact clusters. The

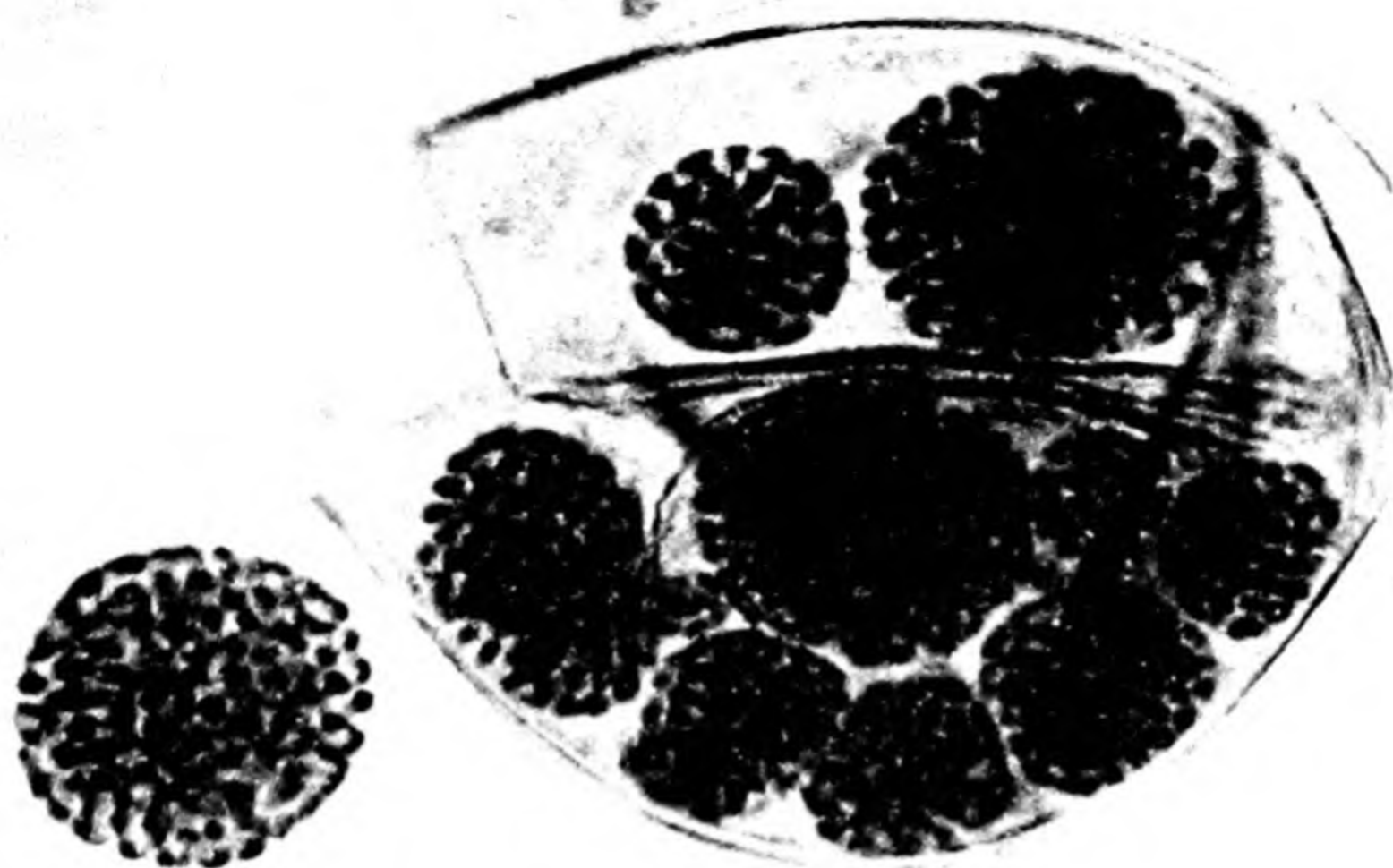


Figure 98. Sporocyst of *Ascospaera apis* containing spore balls. Courtesy Spiltoir and Olive, 1955, *Mycologia*, 47:238-244.

walls of the individual asci disintegrate, but each cluster of asci forms a membrane so that many ascus clusters become delimited within the nutriocyte. The wall of the nutriocyte thickens and becomes pigmented. The mature structure is a spore cyst.

family GYMNOASCACEAE

The Gymnoascaceae are proving to be a most important group, for more and more studies (Stockdale, 1961; Dawson and Gentles, 1961) are showing that some members of this family constitute the perfect stages of dermatophytes, *i.e.*, fungi which cause skin diseases of man and animals. Examples of dermatophytes which belong in this family are *Arthroderma quadrifidum*, *Nannizzia obtusa*, and *Nannizzia incurvata*, among others. Many, perhaps most, members of this family, however, are saprobes, growing on such substrata as leather, dung, and feathers.

In the genus *Byssochlamys* the ascocarp—if we may call it that—

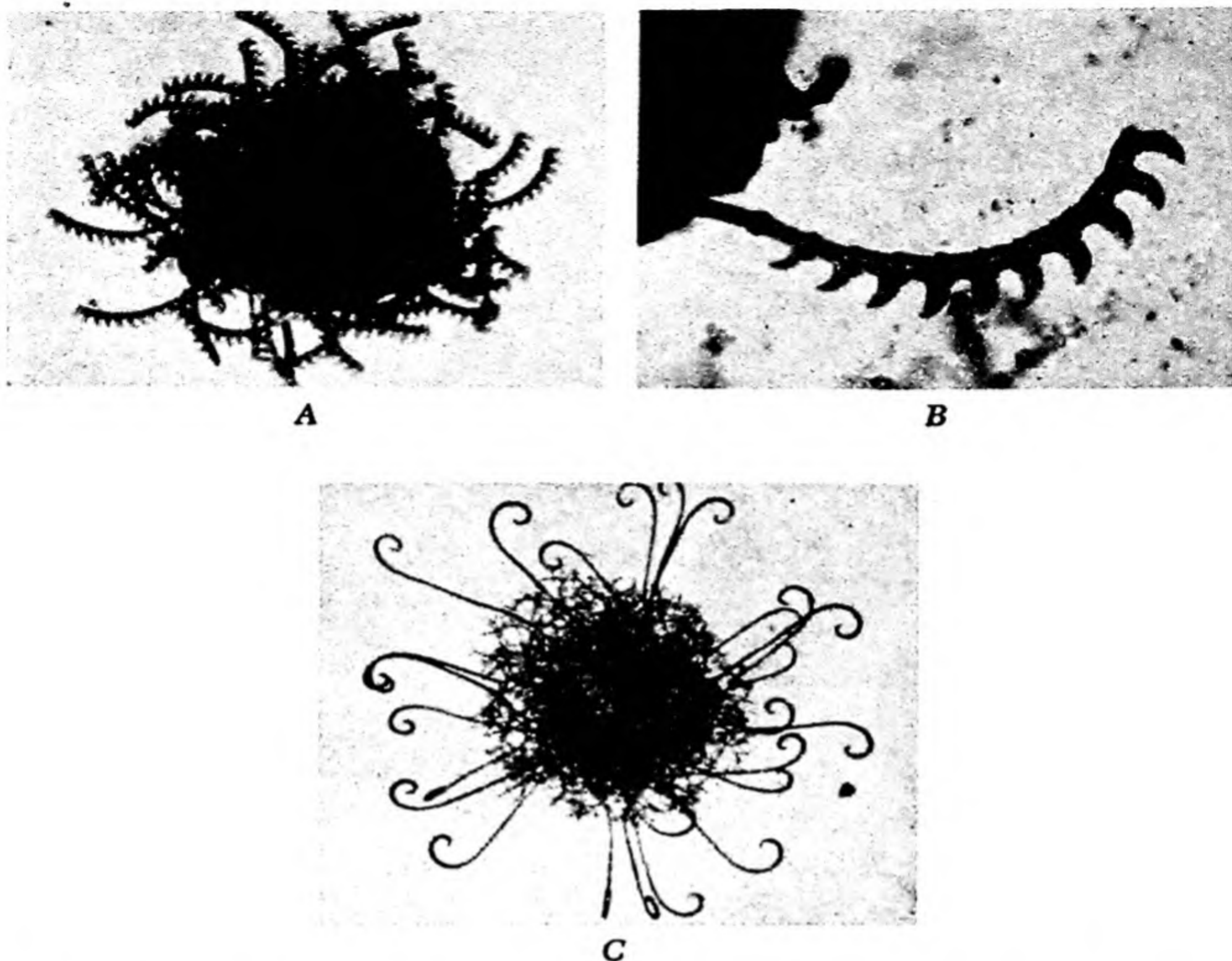


Figure 99. Gymnoascaceae. A. *Ctenomyces serratus* cleistothecium. B. Enlarged view of one of the appendages. C. *Myxotrichum chartarum* cleistothecium. Courtesy Benjamin, 1956, *El Aliso*, 3:301–328.

is nothing more than a cluster of asci without any kind of enclosing peridium. In all other genera the ascal clusters are surrounded by a lax network of hyphae making up a loosely woven cleistothecium, with or without characteristic appendages of various types (Figure 99). Such appendages are useful in distinguishing among the twelve genera in this family (Benjamin, 1956; Kuehn, 1958; Stockdale, 1961).

The globose or pear-shaped asci are irregularly arranged within the cleistothecia. Their walls are evanescent. Eight spores are produced in each ascus. Both homothallic and heterothallic species have been found.

Asexual reproduction takes place by means of blastospores, conidia, or chlamydospores. There seems to be no definite correlation between characters of the perfect stage and types of conidia produced.

The Gymnoascaceae grow well in artificial culture and sporulate under favorable conditions. However, with some pathogenic spe-

cies it is necessary to bait the cultures with hair or other animal structures. Temperatures above 25° C. inhibit sexual reproduction in some species (Dawson and Gentles, 1961).

family EUROTIACEAE

The Eurotiaceae are among the most widely distributed fungi. The family includes a number of genera, most of them having well-formed cleistothecia with definite peridia. Among these genera are three—*Eurotium*, *Sartorya*, and *Emericella*—whose conidial stages are of the *Aspergillus* type (Figure 100). Chiefly because of these connections, the Eurotiaceae are of considerable importance and have been studied intensively.

The conidial stages referable to the form-genera *Aspergillus* and *Penicillium* are so distinct and so well known that it is probably better to discuss these fungi on that basis rather than on the basis of their perfect stages.

form-genus ASPERGILLUS

In their treatise on this form-genus, Thom and Raper (1945) recognize 78 species of *Aspergillus*. The black aspergilli or *Aspergillus niger* group are the fungi which we commonly call black mold. The genus is widely distributed from the arctic region to the tropics. The air everywhere seems to contain the conidia of these organisms, as you can see for yourself by exposing to the air for a few minutes a Petri dish¹ containing a suitable medium.² The soil, too, contains the spores of the aspergilli, but whether these organisms play an important role in soil economy no one has determined with certainty.

The aspergilli are capable of utilizing an enormous variety of substances for food because of the large number of enzymes that they produce. Indeed, it is difficult to find a substance containing some organic matter and a little moisture on which the aspergilli cannot grow. Thus, the aspergilli affect our welfare in a variety of ways. *Aspergillus niger* and several other species are often found on exposed foodstuffs, and cause decay. They also cause considerable trouble as

¹ A Petri dish is a glass container consisting of a circular, flat dish with vertical sides, and a similar but slightly larger cover which fits over it.

² Medium (pl. media) is a term used to designate the common substratum which is used in the laboratory for growing microorganisms. Media may be solid or liquid. For Petri dish cultures, solid media are used. These consist of various food substances, such as sugars, peptones, and mineral-supplying salts, dissolved in distilled water and solidified with 1½–2 per cent agar.

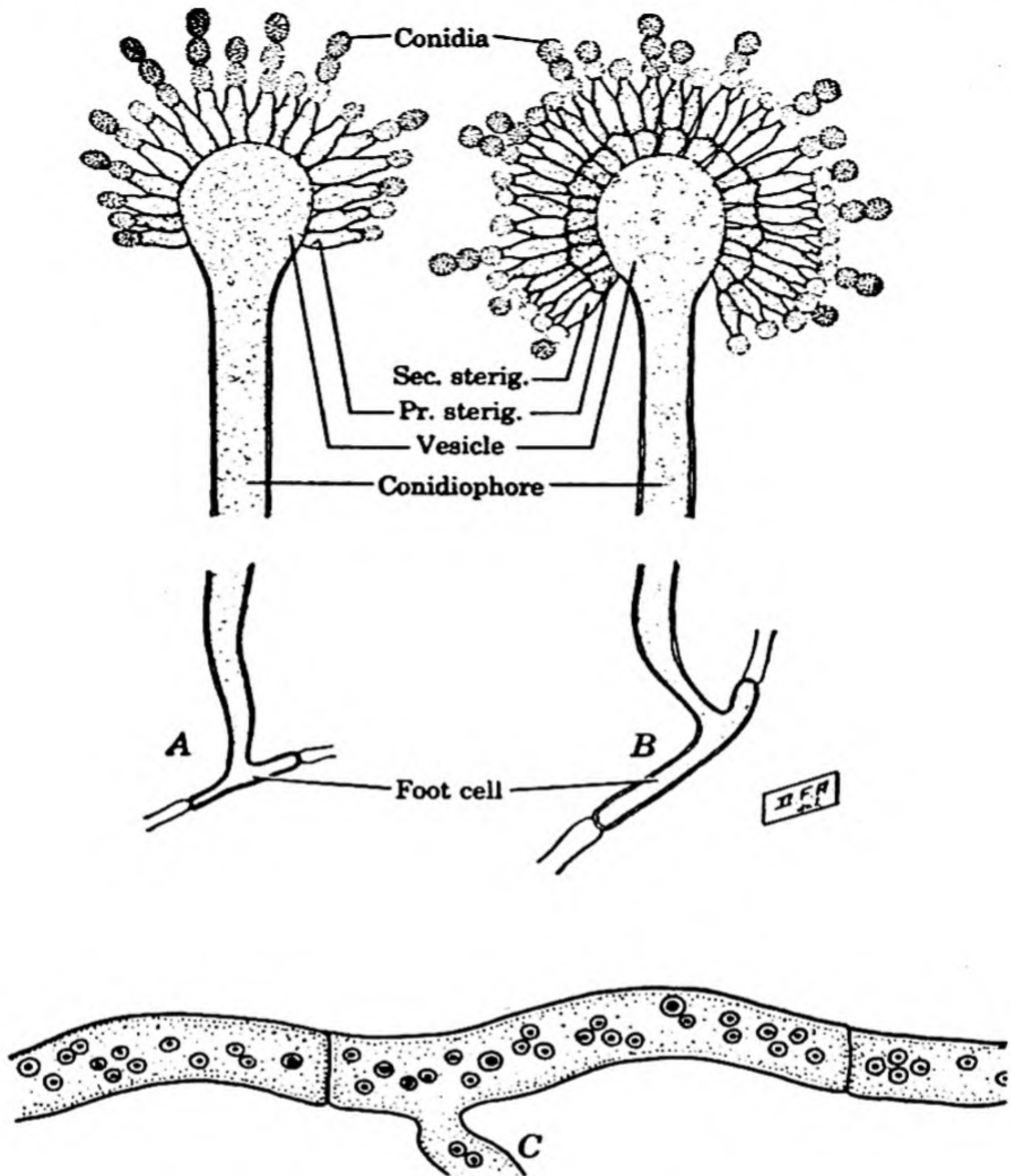


Figure 100. Conidiophores and hypha of *Aspergillus*. A. Conidiophore with one row of sterigmata. B. Conidiophore with two rows of sterigmata. C. Hypha showing multinucleate condition. A, B, by permission, from *A manual of the aspergilli*, by Charles Thom and K. B. Raper, 1945, Williams & Wilkins Co., Baltimore; C, redrawn from Miss Dale, 1909, *Ann. Mycol.*, 7:215-225.

common contaminants of cultures in bacteriological and mycological laboratories. Several species grow on leather and cloth fabrics, reducing their commercial value and imparting a musty odor to shoes and clothing. In tropical climates, where aspergilli are especially troublesome, people have to keep their wardrobes as dry as possible to prevent shoes and clothing from being covered with a heavy

growth of *Aspergillus*. It is a common custom in such regions to have all wardrobes especially wired so that one or more electric light bulbs can be kept burning all the time to keep the atmosphere dry.

Aspergillus fumigatus,¹ *Aspergillus flavus*, *Aspergillus niger*, and other species are animal and human pathogens which cause a group of diseases collectively known as **aspergilloses** (sing. **aspergillosis**). Skinner, Emmons, and Tsuchiya (1947, pp. 206–210) have summarized well our knowledge of this condition. According to them, although aspergillosis of the lungs is much more prevalent in birds, it also occurs in cattle, sheep, horses, and, more rarely, in man. The symptoms closely resemble those of tuberculosis, and it is probable that some doctors have mistakenly diagnosed this disease as tuberculosis. Finegold *et al.* (1959) give a detailed review of twelve cases. In addition to pulmonary aspergillosis, the same species of *Aspergillus* sometimes cause ear infections which may become quite serious.

Because of their great enzymatic activities, aspergilli are employed in several industrial processes. Citric and gluconic acids are manufactured commercially by the use of *Aspergillus niger*. Many other acids and various other chemicals are produced in large or small quantities by members of this genus. Enzyme preparations are made commercially through the use of these fungi, and a number of antibiotics have been isolated from *Aspergillus* cultures, though none has proved equal to penicillin or to the actinomycete products in therapeutic properties. In Japan, *Aspergillus oryzae* is used to make sake, an alcoholic beverage concocted from rice, and to manufacture various fermented foods. In Java, *Aspergillus wentii* is employed in processing soybeans because of its ability to loosen the hard tissues of the bean (Gäumann and Dodge, 1928, pp. 174–175).

Somatic Structures. The mycelium of the aspergilli resembles that of many other fungi. The hyphae are well developed, profusely branched, septate, and hyaline; their cells are, as a rule, multinucleate (Figure 100C).

A voluminous literature has accumulated on the physiology of growth and reproduction and on the biochemistry of enzyme production and activity of the aspergilli. For pertinent references, the student is referred to the standard books on fungal physiology (Foster, 1949; Lilly and Barnett, 1951; Cochrane, 1958; Hawker, 1957; Gray, 1959; etc.). Of particular importance are the researches of Steinberg (1919; 1935; 1945*a*, *b*; 1946) on the mineral requirements of *Aspergillus niger*.

¹ *Sartorya fumigata*.

Asexual Reproduction. While still young and vigorous, the mycelium produces an abundance of conidiophores. These are not organized in any way, but arise singly from the somatic hyphae. The hyphal cell which branches to give rise to the conidiophore is called the **foot cell**. The conidiophores are long, erect hyphae, each terminating in a bulbous head, the **vesicle**.

As the multinucleate vesicle develops, a large number of sterigmata are produced over its entire surface, completely covering it. One or two layers of sterigmata may be produced, according to the species. Thom and Raper (1945) designate the sterigmata in the first layer as primary, and those of the uppermost layer as secondary. When two layers of sterigmata are produced, the secondary are naturally the ones from which the conidia arise. The conidium-bearing sterigmata, whether primary or secondary, are typically bottle-shaped (Figures 100A, B).

As the sterigmata reach maturity, they begin to form conidia at their tips, one below the other, in chains. The conidia are typically globose and unicellular with externally roughened walls. At first uninucleate, in many species they soon become multinucleate by successive nuclear divisions; in most species, however, the conidia remain uninucleate (Yuill, 1950).

The conidia of *Aspergillus* are formed inside the tip of the sterigma, which is actually a tube. A portion of the protoplasm with a nucleus at the tip of the sterigma is delimited by a septum. The protoplast rounds off, secretes a wall of its own within the tubular sterigma, and develops into a conidium. The conidial wall may fuse partially or completely with the wall of the sterigma. In the meantime a second protoplast below the first develops into a spore and pushes the first spore outward without disjunction, so that a chain of spores is formed as the sterigma protoplasm continues to grow and cut off more conidia one below the other.

Because conidiophores and conidia are produced in such abundance, their color is the predominant one of the colony which they cover. *Aspergillus* colonies thus appear to be black, brown, yellow, green, and so on, the color depending on the species and on the medium on which the fungus is growing. Since the color of the colony is one of the criteria for identification, we cannot overemphasize the importance of using a standard growth medium of known chemical composition, and standard conditions for growing aspergilli. Pigment production in *Aspergillus* is profoundly influenced by the presence or absence of minute quantities of the so-called trace ele-

ments. So sensitive are these fungi that *Aspergillus niger* is used to detect copper, in soils and other substances, in amounts which are too small to be determined by chemical methods. Mulder (1938) determined that 2.5 millionths of a gram of copper is sufficient to induce maximum depth of color in this organism. When the copper content falls below this amount, the color of the conidia is proportionately lighter, and in the almost complete absence of copper the normally dark brown to black conidia appear yellow.

Sexual Reproduction. The perfect stages of most species of *Aspergillus* have not been discovered, and it is likely that such species have lost their ability to reproduce sexually. This appears the more probable in view of the fact that students of these fungi have found evidence of sexual degeneration even in species which do form asci. The work of a number of investigators shows that the sexual behavior of different species of *Aspergillus* varies considerably, from apparently normal plasmogamy between two functional gametangia to a complete absence of an antheridium, and the development of the asci from the ascogonium alone. Professor Ernst Gäumann of Zürich, Switzerland, who is one of the foremost European mycologists, gives a thorough discussion of the sexual pattern of the Eurotiaceae in his book *The Fungi* (1952).

Sexual reproduction takes place in several ways and results in at least five different types of ascocarps. Three of these types are briefly discussed by C. R. Benjamin (1955), on the basis of which he recognizes the three ascomycetous genera *Eurotium*, *Sartorya*, and *Emericella*, all species of which produce *Aspergillus*-type conidia.

In *Eurotium* the sex organs, antheridia and ascogonia, are produced close to each other on somatic hyphae. Both are multinucleate, elongated structures. Often helical, they coil around each other. Whether or not the antheridium is functional, a pairing of nuclei takes place in the ascogonium. If nuclei from the antheridium have entered, they pair with the ascogonial nuclei; otherwise the ascogonial nuclei themselves approach each other in pairs. After the pairing of the nuclei, the ascogonium produces a number of ascogenous hyphae which branch within the developing ascocarp. The branches are of different lengths, and the asci which are formed at their tips are produced at different levels.

At an early stage, the cleistothecium begins to develop as a single layer of cells around the sex organs. It matures into a small, globose ascocarp with smooth walls, which is generally yellow. The asci are globose, ovoid, or pear-shaped. They are evanescent, dissolving

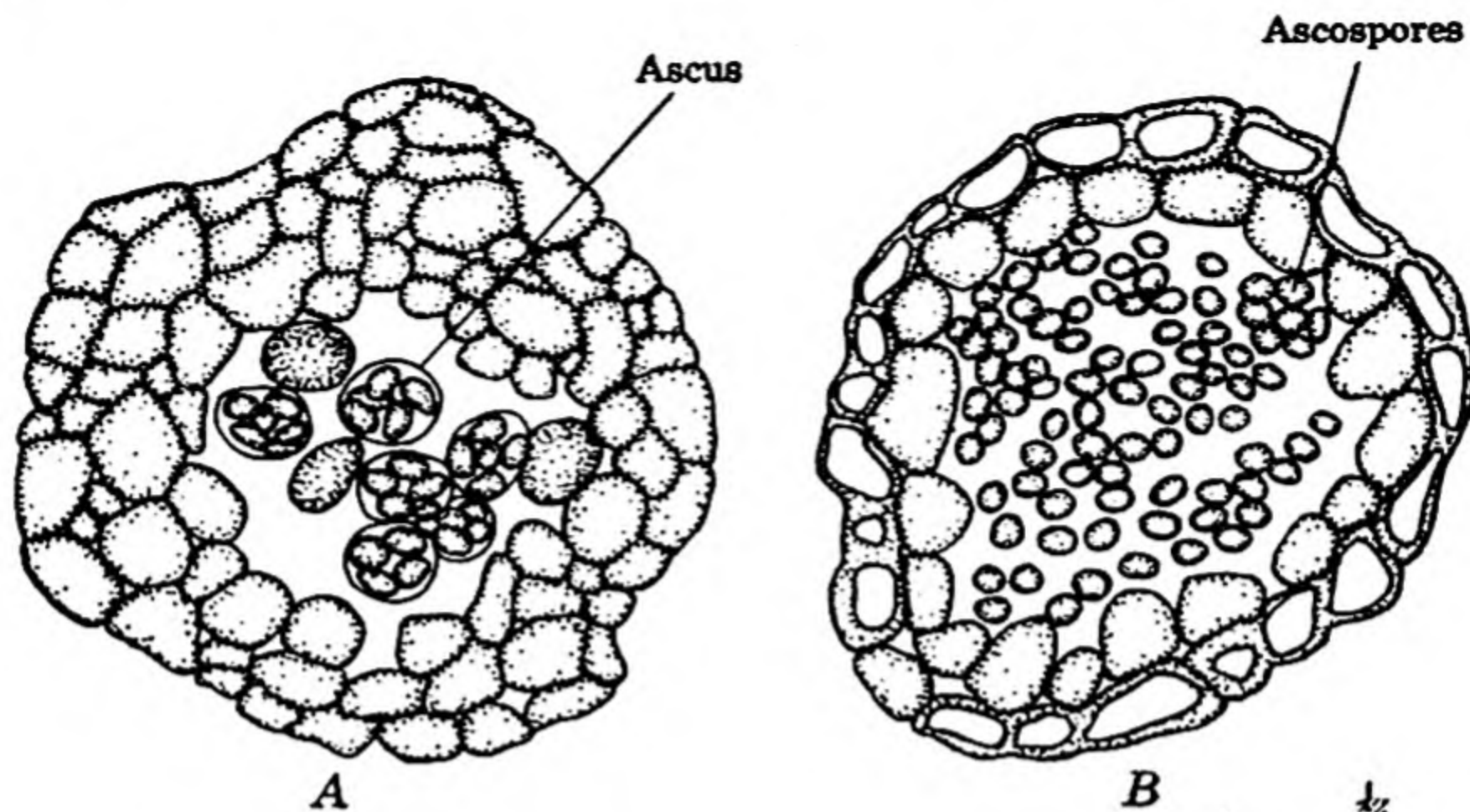


Figure 101. *Eurotium* sp. Cross section of two cleistothecia, one (A) showing asci, the other (B) after the asci have disintegrated.

away soon after ascospore formation, leaving the ascospores free within the cleistothecium (Figure 101).

In *Sartorya* the ascocarp is initiated by a coiled ascogonium. No antheridium is produced, and development proceeds from the female organ alone. The nuclei which fuse in the ascus mother cell are of ascogonial origin (Olive, 1944). The wall of the cleistothecium is composed of several layers of interwoven hyphae and is enveloped at maturity by a loose network of sterile hyphae which gives the ascocarp the appearance of a cottony ball. The asci are much like those of *Eurotium*.

In *Emericella* no sex organs are formed. The ascocarp appears to originate from a loose hyphal coil. The wall of the cleistothecium consists of several layers of thick interwoven hyphae and at maturity is covered with thick-walled "hulle" cells. These are specialized structures whose origin and function are unknown.

Two other types of perfect stages known in *Aspergillus* cannot be placed in any known ascomycete genus. The more interesting is that of *Aspergillus alliaceus* (Fennell and Warcup, 1959) in which the cleistothecia are formed within a sclerotial stroma which retains its sclerotial character even after the cleistothecia within it are completely mature.

The ascospores in all these types of ascocarps are fundamentally shaped like pulley wheels, although the furrows may be essentially absent in some species. The outside wall of the two halves is vari-

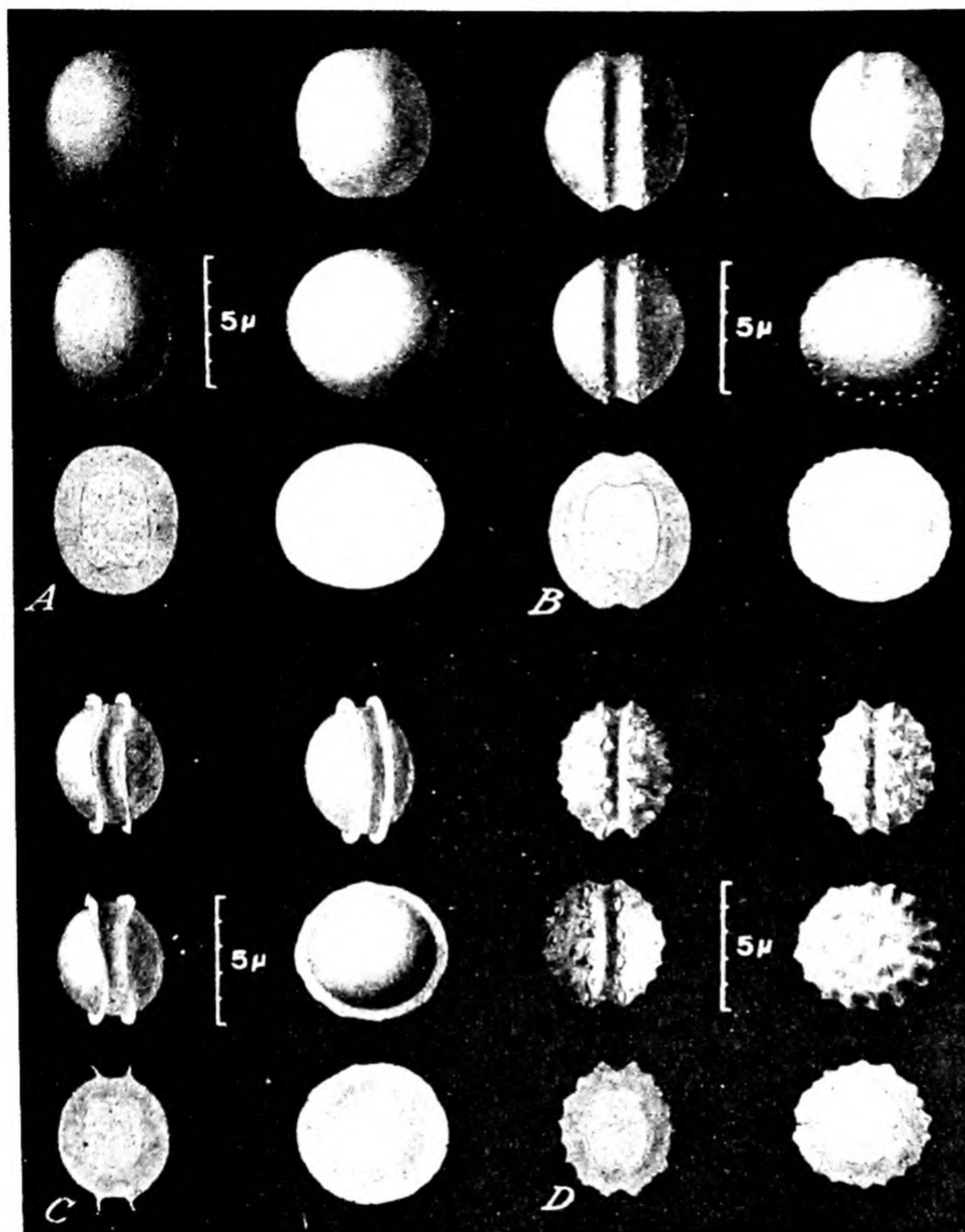


Figure 102. Ascospores of four species of *Eurotium* in side and front views, and in section. By permission, from *A manual of the aspergilli*, by Charles Thom and K. B. Raper, 1945, Williams & Wilkins Co., Baltimore.

ously modified and sculptured, so that, while the edge view gives the appearance of a pulley wheel, in face view the ascospore may appear round, scalloped, star-shaped, and so on (Figure 102). Eight ascospores are usually produced in each ascus, but often we find fewer. Upon germination, the ascospores give rise to germ tubes which develop into mycelia.

Parasexual Phenomena. Much of the information which we have on parasexuality has been obtained through a study of *Emmericella nidulans* (= *Aspergillus nidulans*). We have already mentioned this phenomenon in the introductory chapter on fungi (page 30). We shall discuss the parasexual cycle in more detail in connection with the Deuteromycetes (Chapter 18).

form-genus *PENICILLIUM*

Occurrence, and Importance to Man. The penicillia are as common and as cosmopolitan as the aspergilli. They are the so-called green molds and blue molds which we so frequently find on citrus and other fruits, on jellies and preserves, and on other foodstuffs that have become contaminated with their spores. The conidia of *Penicillium*, like those of *Aspergillus*, are everywhere in the air and in the soil. In the biological laboratory they are as frequent contaminants as *Aspergillus* and *Rhizopus*.

Various species of *Penicillium* attack and destroy fruits. *Penicillium italicum* and *Penicillium digitatum* are common pathogens of citrus fruits, causing blue mold and green mold, respectively. *Penicillium expansum* causes a decay of apples in storage. In destroying leather and fabrics, the penicillia are no less effective than the aspergilli. Some of the penicillia have been found to be associated with animal and human diseases, but in this respect the genus is probably not so important as *Aspergillus*. *Penicillium* sometimes gives trouble in silos, where it spoils large quantities of silage, making it unsuitable for feed.

Many species of *Penicillium* are capable of producing organic acids, such as citric, fumaric, oxalic, gluconic, and gallic. Industrially, the penicillia are important in making cheese and antibiotics. *Penicillium roqueforti* is responsible for the highly prized (and highly priced) flavor of Roquefort cheese, and *Penicillium camemberti* for that of Camembert cheese. Danish blue cheese and the Italian Gorgonzola are also ripened with *Penicillium*. *Penicillium notatum* and *Penicillium chrysogenum* have come to prominence as sources of the now famous antibiotic, penicillin. Although other species of

Penicillium also produce this antibiotic, certain selected strains of the latter species have proved to be most efficient in its manufacture and are being used exclusively in the commercial preparation of this drug (Figure 103). Of great interest in this connection is the ability of mycologists to produce new high-yielding strains of *Penicillium chrysogenum* by subjecting conidia to ultra-violet irradiation and testing the colonies originating from the surviving conidia for penicillin production. Yields of penicillin have been increased enor-

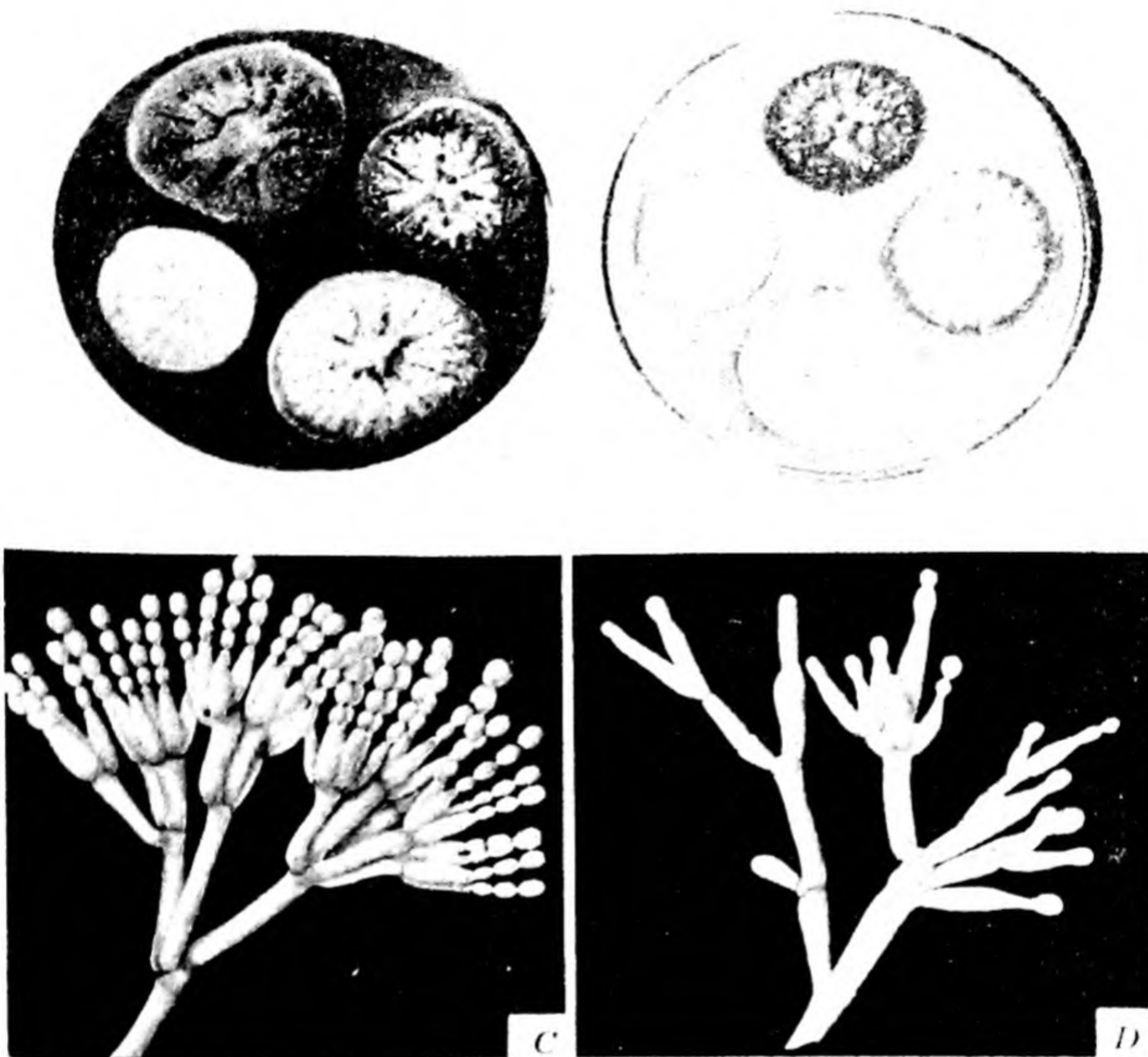


Figure 103. *Penicillium chrysogenum* Thom. A, B. Colonies showing variation of strains. C, D. Conidiophores showing variation in branching between strains. A, B, by permission, from *A manual of the penicillia*, by K. B. Raper and Charles Thom, 1949, Williams & Wilkins Co., Baltimore; C, D, courtesy Raper and Alexander, 1945, *Jr. El. Mitchell Sci. Soc.*, 61:74-113, by permission of the University of North Carolina Press, Chapel Hill.

mously in this way, and this has been a primary factor in the price reduction which has made this first "wonder drug" available to all.

Morphology and Life History. The life history of a typical *Penicillium* is very much like that of *Aspergillus*, but the morphology of the structures differs considerably. The mycelium produces simple, long, erect conidiophores which branch about two thirds of the way to the tip, in characteristic symmetrical or asymmetrical, broom-like fashion (Figure 104). The conidiophore, commonly referred to as the brush, is technically known as the **penicillus** (pl. **penicilli**; L. *penicillum* = small brush). The multiple branching of the conidiophore ends in a group of sterigmata which bear the long conidial chains.

The conidia are globose to ovoid, and under the microscope resemble glass beads. They are formed in the same manner as in *Aspergillus*. The enormous quantities of greenish, bluish, or yellow conidia which are produced are chiefly responsible for the charac-

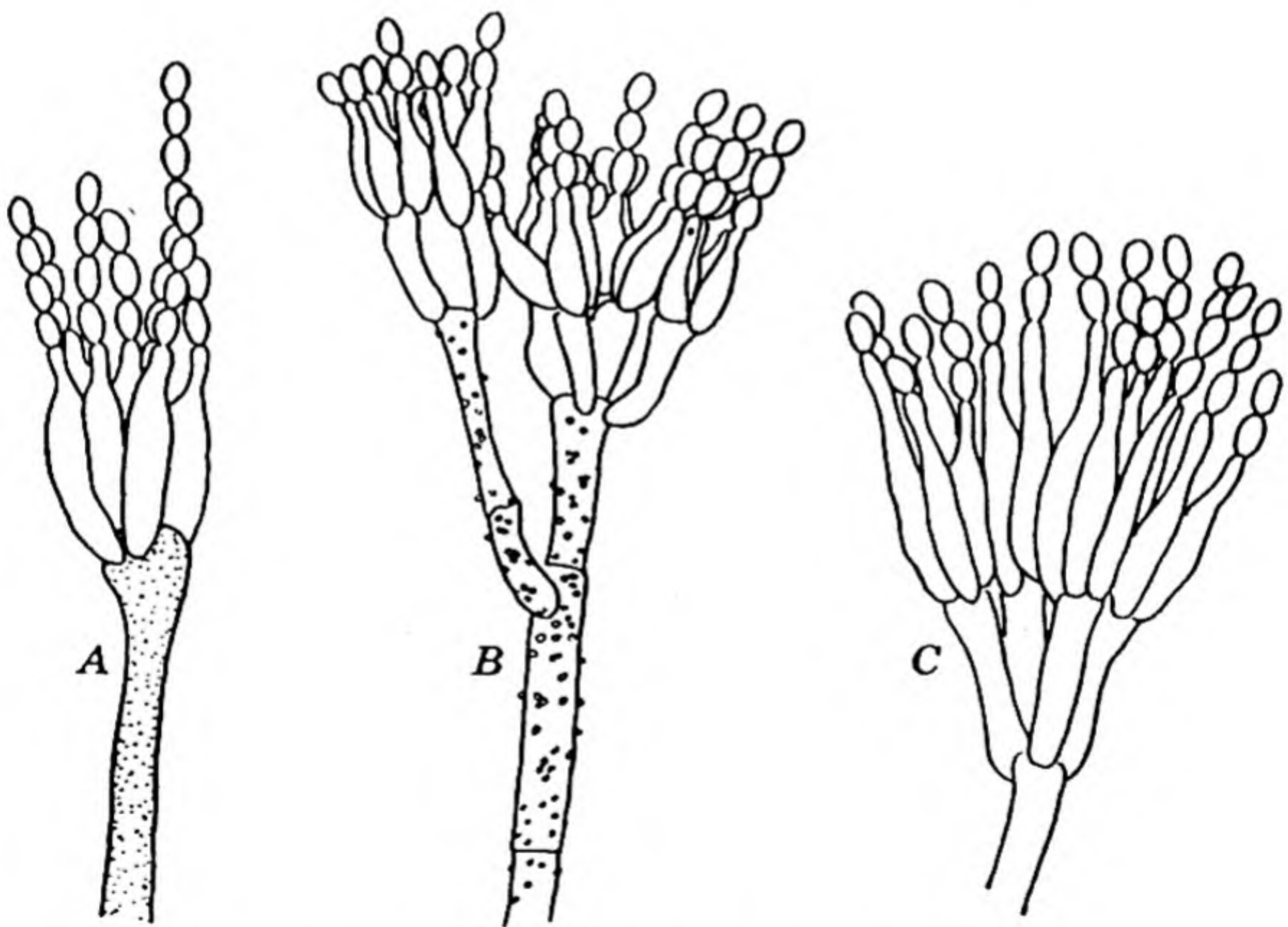


Figure 104. Three types of conidiophores of *Penicillium*. A. *Penicillium thomii*. B. *Penicillium lanoso-coeruleum*. C. *Penicillium wortmanni*. By permission, from *A manual of the penicillia*, by K. B. Raper and Charles Thom, 1949, Williams & Wilkins Co., Baltimore.

teristic colony color of various species of *Penicillium*. The conidia germinate easily into germ tubes from which mycelia develop.

We know nothing about the perfect or sexual stage of most species of *Penicillium*, but the cleistothecia of enough species have been found to give us a clear idea of the sexual stage of these fungi in general.

C. R. Benjamin (1955) recognizes two genera in the Eurotiaceae which have *Penicillium* conidial stages: *Talaromyces* and *Carpenteles*.¹

In *Talaromyces* the ascocarp is of indeterminate growth and may continue increasing in size even after the ascospores begin to mature. The wall of the cleistothecium consists of more or less loosely interwoven hyphae. In some species the asci are formed from croziers; in others they are produced directly from the ascogenous hyphae in short chains.

In *Carpenteles*, the ascocarp reaches a definite size and matures from the center out. Its hard walls consist of thick-walled pseudoparenchyma. The asci are usually borne singly on short branches of the ascogenous hyphae.

Sexual reproduction appears to take place by functional gametangia in some species, but in others the antheridia no longer seem to function. In such species the ascogonial nuclei pair and pass into the ascogenous hyphae. From these hyphae asci develop within the cleistothecium in the usual manner. Such a species is *Talaromyces vermiculatus*, (= *Penicillium vermiculatum*), which Dangeard investigated in 1907 (Figure 105). The uninucleate mycelium bears a uninucleate, elongated ascogonium in which nuclear division occurs several times, resulting in the production of as many as sixty-four nuclei. In the meantime, an antheridium, which generally originates as a uninucleate branch of a separate hypha, climbs spirally up the ascogonium (Figure 105D). At the point where the tip of the antheridium touches the ascogonium, the walls dissolve and the two protoplasts come in contact with each other (Figure 105E). But Dangeard claimed that at no time does nuclear migration take place, and that the antheridial nucleus can still be seen in the antheridium even after the formation of the ascogenous hyphae. Dangeard believed that the paired nuclei in the ascogenous hyphae are derived from the original ascogonial nucleus (Figure 105F). Karyogamy takes place in the ascus mother cells, and the ascospores

¹ For a discussion of the very controversial issue regarding the nomenclature of the perfect stages of *Aspergillus* and *Penicillium* see Raper (1957).

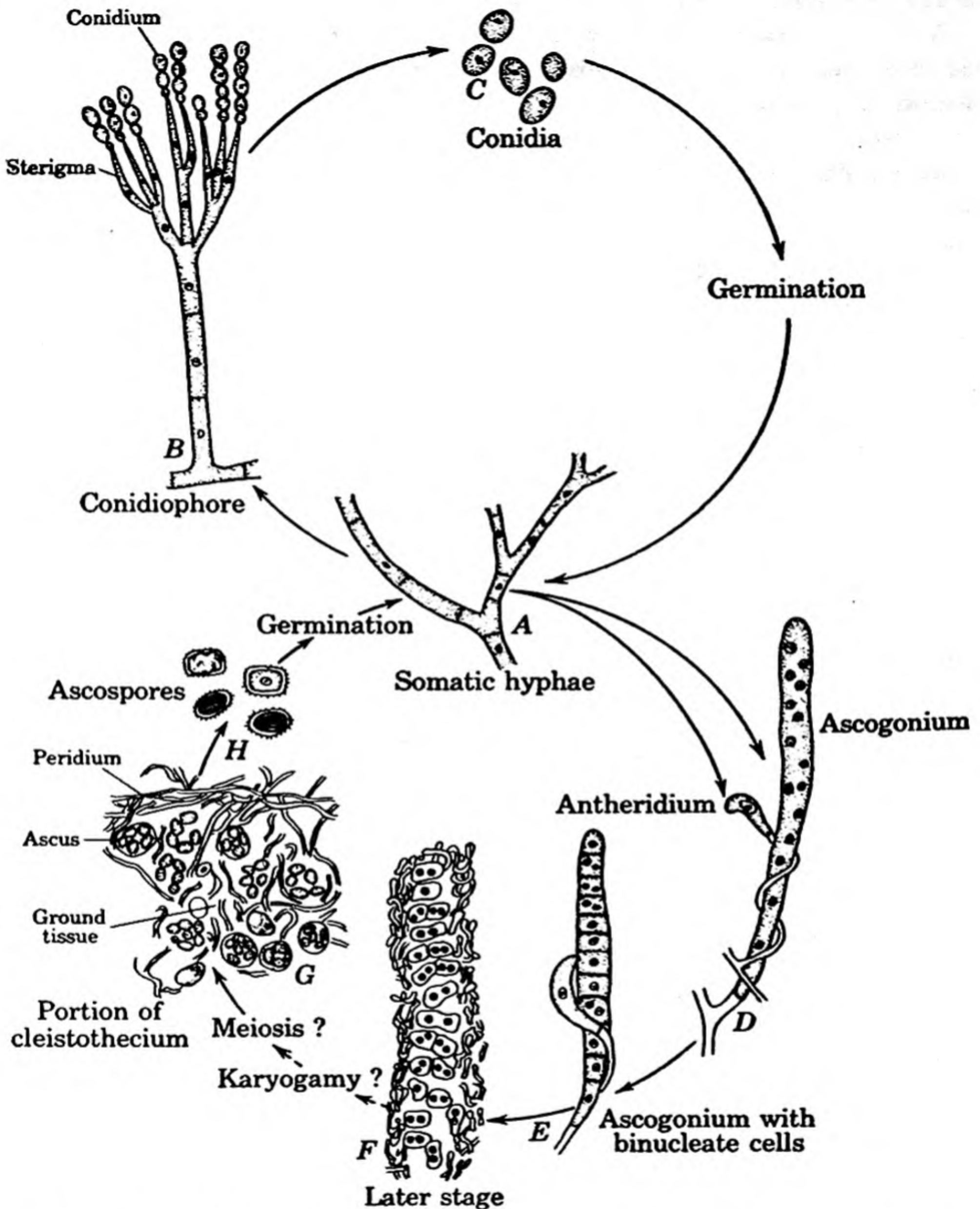


Figure 105. Life cycle of *Talaromyces vermiculatus* (= *Penicillium vermiculatum*). Redrawn from Dangeard, 1907, *Botaniste*, 10:1-385.

develop presumably by meiosis. The asci are scattered at various levels within the cleistothecium. The ascocarp itself develops from somatic hyphae which envelop the sexual apparatus (Figure 105G). The asci, which are globose or pear-shaped, dissolve away soon after ascospore formation, releasing the ascospores, shaped like pulley wheels, into the cleistothecium.

Classification. Drs. Kenneth Raper and Charles Thom have given us an excellent treatise on the penicillia (1949), as they have on the aspergilli. You will find these two manuals indispensable for the identification of members of these form-genera. Given considerable experience with these fungi, mycologists can now identify an isolate of *Penicillium* with a fair degree of accuracy by using the standard media described in the manual—a task which was extremely difficult before that book was published.

order ONYGENALES

This small and little-known order, consisting of the single family Onygenaceae, contains but a few genera. Ciferri (1957), who established the order, divides it into three families: Onygenaceae, Dendrosphaeriaceae, and Trichocomoidaceae.¹ Most authors do not recognize this order, but treat its members under two families, Onygenaceae and Trichocomaceae,¹ which they place in the Eurotiales.

The ascocarp is a stalked *mazaedium* (pl. *mazaedia*; Gr. *maza* = dough + *eidos* = like). This is a fruiting body in which the spores, freed from the asci, form a powdery mass. In the Onygenales, globose or pear-shaped asci are scattered within the globose head of the ascocarp. The ascus walls dissolve away, and some of the disintegrated tissue forms a capillitium which, together with the spores, is extruded in a powdery mass.

The genus *Onygena* grows on dead animal matter such as hair, feathers, hoofs, and horns. *Onygena equina* is a cosmopolitan species. *Trichocoma* and *Dendrosphaera* are tropical monotypic genera growing on dead wood (Boedjin, 1935).

order MICROASCALES

The Microascales produce their asci in beaked perithecia with definite ostioles through which the ascospores are discharged. Two families are now included in this order, the Microascaceae and the Ophiostomataceae. We shall discuss only the latter.

¹ Note difference in spelling.

family OPHIOSTOMATACEAE

The Ophiostomataceae include the genus *Ceratocystis*, in which a number of economically important fungi belong. Whether other genera should be included in this family is a question which has not been settled. Among the plant parasites are *Ceratocystis fagacearum*, the cause of oak wilt; *Ceratocystis ulmi*, the cause of Dutch elm disease; and *Ceratocystis fimbriata*, the cause of sweet potato black rot. Several species of *Ceratocystis*, such as *Ceratocystis pilifera* and *Ceratocystis minor*, are responsible for "blue stain," which greatly reduces the commercial value of lumber.

The Ophiostomataceae are easily recognized by their superficial or only partially buried perithecia with their globose bases and their greatly elongated necks which are several times the diameter of the perithecium in length, and end in a shredded, feathery tip. The ascus walls gelatinize early in perithecial formation, and the ascospores are exuded through the long neck of the perithecium, embedded in mucus which forms a droplet at the ostiolar opening. Ascospores vary in shape from ovoid to crescent-shaped to hat-shaped (Hunt, 1956).

In the Eurotiaceae we noted an absolute correlation between certain ascomycetous genera and their conidial stages. All species of *Eurotium*, for example, have the same type of conidia, formed in essentially the same way. Furthermore, the conidial stages of all known species of *Eurotium*, *Emericella*, and *Sartorya* are similar enough to be recognized as belonging to the imperfect form-genus *Aspergillus*. In the genus *Ceratocystis* of the Ophiostomataceae we have an example of the opposite extreme. Not only may different species have entirely different conidial stages, but also one and the same species may produce two kinds of conidia which bear no resemblance to each other.

Two general types of conidia are produced in the Ophiostomataceae: endoconidia (Figure 106) and exoconidia. An **endoconidium** (Gr. *endos* = inside + *conidium*) is formed inside a hypha and slips out. An **exoconidium** (Gr. *exo* = outside + *conidium*) is formed on the surface of a hypha by any one of several methods.

In *Ceratocystis ulmi* and some other species, **synnemata** (sing. **synnema**; Gr. *syn* = together + *nemma* = yarn) are formed. A synnema is a group of conidiophores cemented together to form an elongated, spore-bearing structure. This may be split in different ways near the apex, sometimes resembling a feather duster. In *Ceratocystis ulmi* the synnemata are black, elongated bodies that

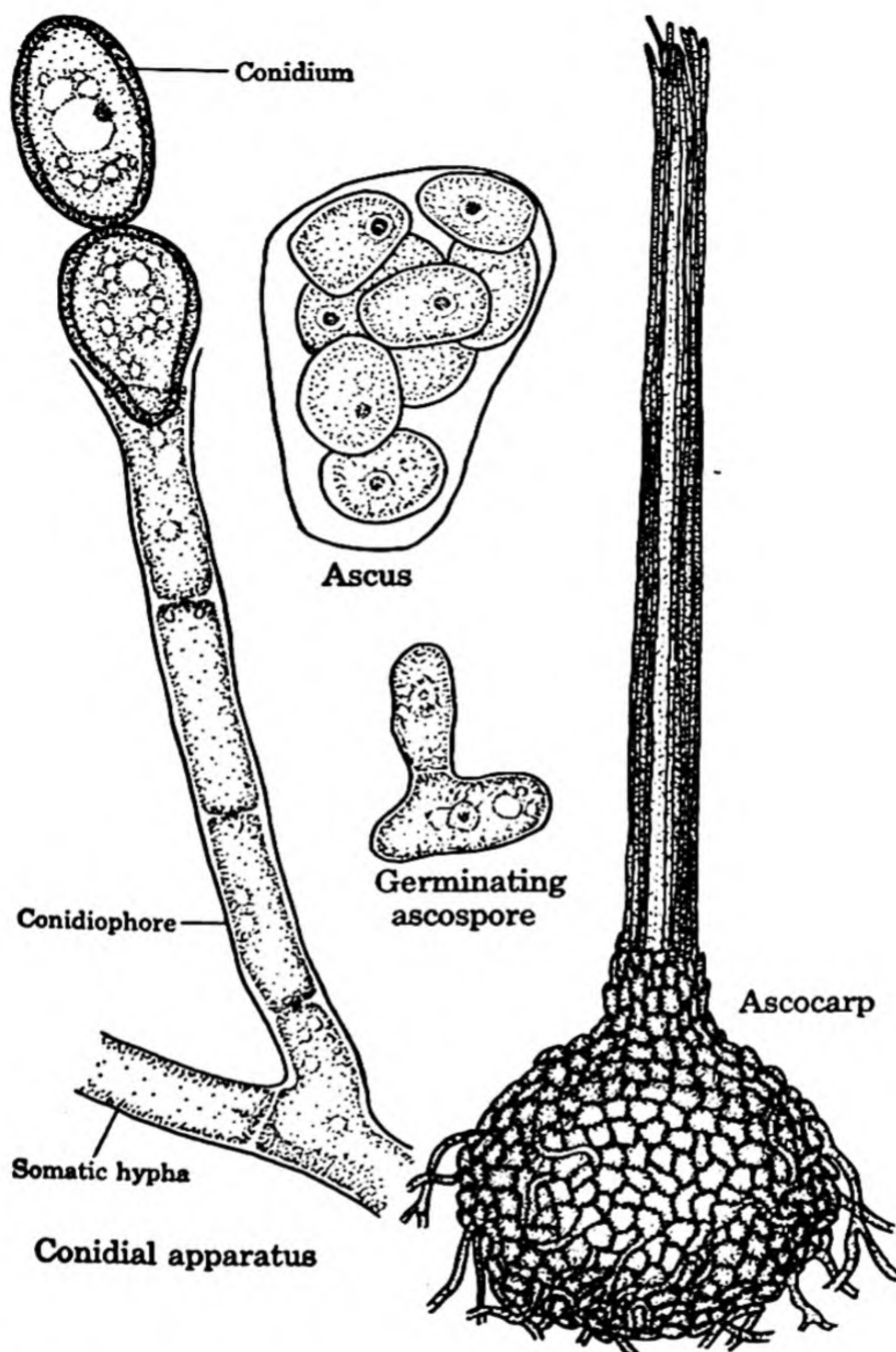


Figure 106. *Ceratocystis fimbriata*. Redrawn from Andrus and Harter, 1933, *Jr. Agr. Res.*, 46:1059-1078.

look like bristles and bear colorless conidia at their tips. This type of conidial apparatus is characteristic of the form-genus *Graphium* (see page 417). *Ceratocystis ulmi* also produces conidia on short conidiophores. These are cut off one after the other and are held together by a drop of mucus forming a globose, glistening head. Such a conidial stage belongs to the form-genus *Cephalosporium*. *Ceratocystis fimbriata* and *Ceratocystis fagacearum* are two species which produce endoconidia. When a conidium is about to be formed, the hyphal protoplasm at the tip of the hypha secretes a second wall, separate from the hyphal wall, and cuts off conidia which are then liberated in chains, one after the other, from the tip of the hyphal tube (Figures 106, 107).

The life cycle of the oak wilt organism *Ceratocystis fagacearum* is fairly well known. The well-developed mycelium produces rectangular endoconidia formed at the tips of the hyphae and extruded one after the other (Figure 107). These are capable of germinating and reproducing the fungus asexually, or of behaving as spermatia and thus playing an important role in sexual reproduction. The fungus is heterothallic (Bretz, 1951, 1952). Some details of sexual reproduc-



Figure 107. Endoconidia of *Ceratocystis fagacearum*. Note how the conidia which have issued from each conidiophore cling together. Photomicrograph by the author.

tion have been worked out (Wilson, 1956). The ascogonium is born naked. As it develops, it becomes enveloped by hyphae. Its tip cell, the trichogyne, produces long branches which probably act as receptive hyphae. When conidia of the opposite mating type are sprayed on the culture, perithecia develop. It is probable that the conidia fuse with the trichogyne branches and that their nuclei migrate into the ascogonium. Typical ascogenous hyphae or croziers are not formed. Instead, the ascogonium produces chains of ascogenous cells after spermatization has been accomplished.¹ These differentiate into usually binucleate cells in which karyogamy and meiosis take place. The ascogenous cells are in reality protoplasts because they are devoid of cell walls, being enveloped only by a very thin membrane. A third nuclear division, following meiosis, produces eight nuclei around which the cytoplasm cleaves, resulting in a mass of eight ascospores. Ascospores are extruded in a drop of liquid from the tip of the long beak characteristic of the perithecia of *Ceratocystis*. In nature, perithecia are produced on mycelial mats formed between the wood and the loosened bark of oak trees which have been killed by the fungus (Stessel and Zuckerman, 1953). Stambaugh *et al.* (1954) have found 18–24° C. to be the optimum temperature range for production of perithecia in culture.

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¹ The term spermatization refers to the contact of detached cells (spermatia, microconidia, conidia, oidia, etc.) and trichogynes.

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14 series PYRENOMYCETES the perithecial fungi

Introduction. The Pyrenomycetes are Ascomycetes, most of which bear unitunicate, club-shaped or cylindrical asci, in virtually closed ascocarps which in the majority of species have a round pore through which the ascospores are expelled at maturity.

Typically, the ascocarp of the Pyrenomycetes is a globose or flask-shaped perithecium. Exceptionally, it may be a cleistothecium or even an ascostroma.¹

A perithecium, regardless of whether it is associated with a stroma or not, has a true wall of its own. The pore through which the ascospores escape is the opening of a true **ostiole** (L. *ostiolum* = little door) formed schizogenously and lined with **periphyses** (sing. **periphysis**; Gr. *peri* = around + *physis* = a growth). These are short hair-like growths in the form of a fringe lining the inner walls of the perithecial neck.Periphyses, however, may also line the lysigenous pores formed in ascostromata.

Next in importance to the structure of the ascus in denoting probable relationships is the character of the **centrum** (pl. **centra**; Gr. *kentron* = center). The centrum, as defined by Wehmeyer (1926), who first used this term, refers to "the totality of structures within the perithecial wall." This includes the asci, any sterile structures, such as the paraphyses or pseudoparaphyses which may be present, and the inner portion of the ascocarp wall. Thus, the various combinations of stroma, perithecial wall, ostiole, paraphyses, and other sterile structures, and the method of the development of these various structures, are the criteria we use to subdivide the Pyrenomycetes into orders. The numerous studies on the structure of the Pyrenomycetes by von Höhnelt, Petrak, Wehmeyer, Nannfeldt, Mil-

¹ See page 265 for a more inclusive definition of the Pyrenomycetes.

ler, Luttrell, Müller, von Arx, etc., have contributed enormously to the understanding of this most difficult group. Although there is no general agreement as to the relationships of these fungi, or indeed as to the definition of all the major orders, certain fundamental principles are being discovered which will eventually, we hope, lead to better agreement. It would be confusing to the beginning student to be presented with the various viewpoints on this very controversial subject. Suffice it to point out here that no agreement exists on the classification of these fungi and that the view which I am presenting here is one of several.

On the basis of present-day information we may accept nine orders as validly belonging to the Pyrenomycetes. These are the Erysiphales, Meliolales, Chaetomiales, Clavicipitales, Diaporthales, Sphaeriales, Hypocreales, Coronophorales, and Coryneliales. If you will consult the key to the orders of the Euascomycetidae on page 265, you will note at a glance the important differences between these orders.

order ERYSIPHALES

The Erysiphales are often included in a discussion of the Plectomycetes because most of them have a completely closed ascocarp (cleistothecium). However, since we have taken the view that one of the chief characteristics of the Plectomycetes is that their asci are scattered, we must consider the Erysiphales as Pyrenomycetes.¹

The Erysiphales have large, globose or ovoid, often stalked asci which, at maturity, form a single basal layer or tuft within a cleistothecium. The cleistothecial wall is pseudoparenchymatous and dark. The asci are persistent. No sterile threads are formed in the ascocarp. As the asci develop, they expand at the expense of the pseudoparenchymatous cells of the centrum and eventually fill the cleistothecial cavity.

The Erysiphales form their ascocarps on a superficial mycelium without the development of a stroma. Since all attempts to grow them in artificial culture on non-living media have failed, we must regard them at present as obligate parasites.

The order is subdivided into various numbers of families by different authors. As delimited here, the order Erysiphales includes the single family Erysiphaceae.

¹ Luttrell (1951) points out, however, that in the early stages of development the asci of the Erysiphales form an irregular layer across the middle of the ascocarp extending to different levels at both the base and the apex.

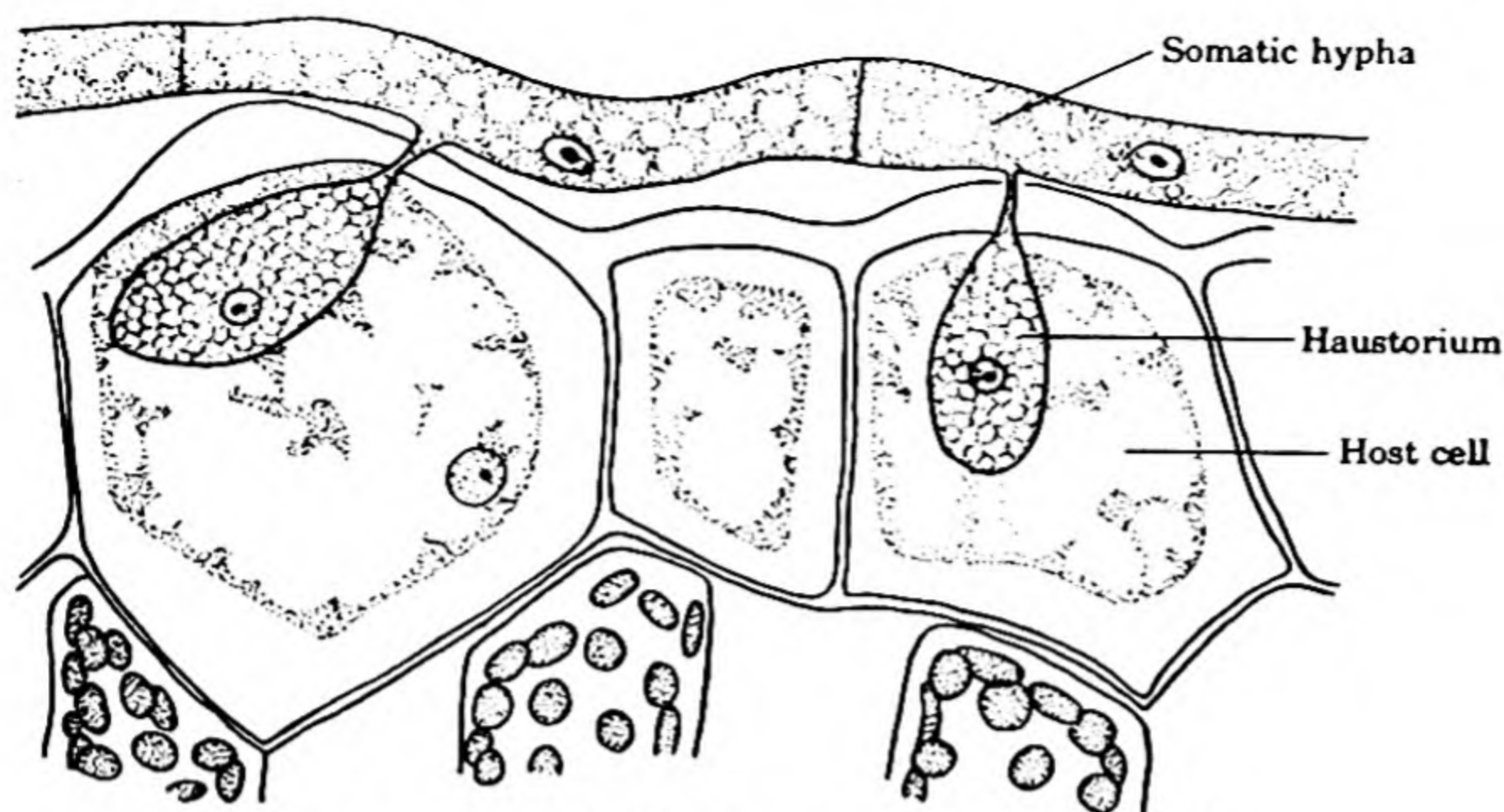
family ERYSIPHACEAE

Occurrence, and Importance to Man. The Erysiphaceae cause a group of plant diseases commonly known as powdery mildews, a designation they have earned because of the enormous number of conidia produced on the surface of the host. These appear to the unaided eye as a white, powdery coating.

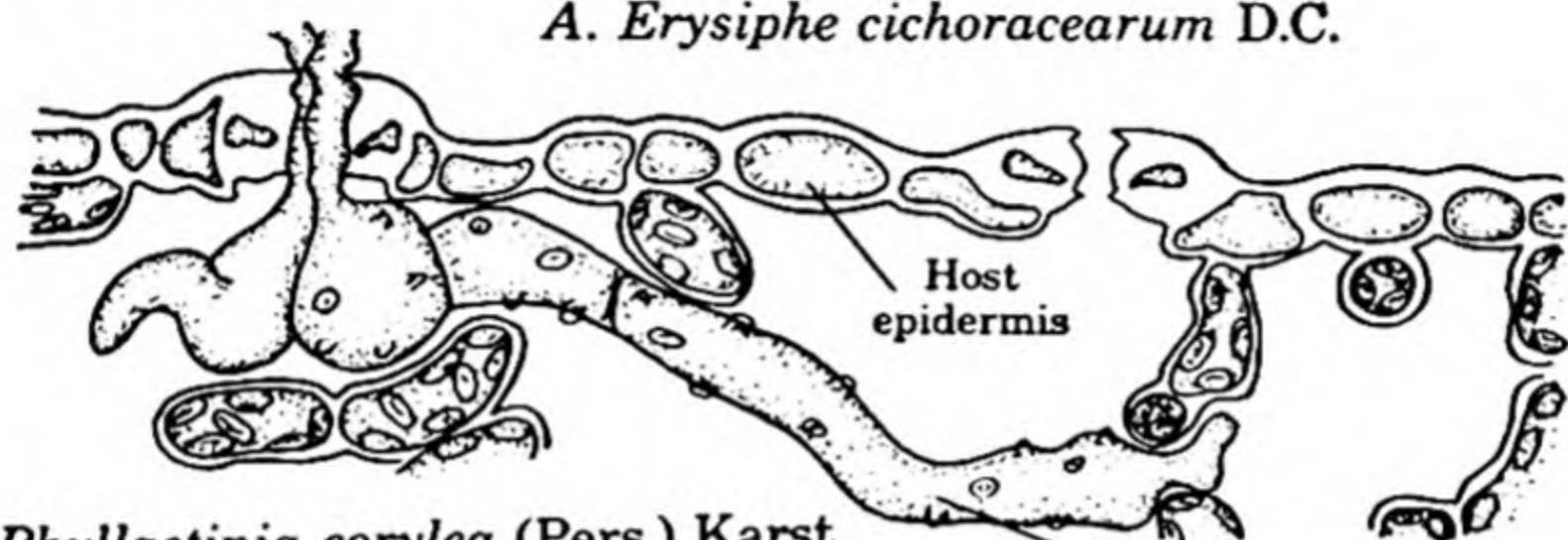
In their parasitism some of the Erysiphaceae are almost omnivorous, as shown by such species as *Erysiphe polygoni*, which Salmon (1900) reported as having been recorded on 352 host species. On the other hand, *Podosphaera leucotricha* attacks only apple (*Pyrus malus*) and Toringo crab (*Malus sieboldii*), and there are at least eight other species of powdery mildews, each of which is known to attack only its own special host. In this last group is *Sphaerotheca phytoptophila*, the most specialized of powdery mildews which Salmon discusses. He states that this species attacks only the galls of western hackberry (*Celtis occidentalis*) which are caused by a species of *Phytoptus*, a mite. Careful cross-inoculation studies have established that certain species of powdery mildews consist of a number of physiological races, each with a limited host range (Mains and Dietz, 1930; Yarwood, 1936; Schmitt, 1955).

Some of the plant diseases caused by members of this family are among the most destructive ones known, whereas others appear to be very mild and cause little damage. Among the most serious parasites are *Uncinula necator*, the cause of powdery mildew of the grape vine, which under conditions favorable to the fungus can result in the complete destruction of the entire crop in a region; *Sphaerotheca mors-uvae*, powdery mildew of gooseberries; *Sphaerotheca pannosa*, powdery mildew of roses; *Podosphaera leucotricha*, powdery mildew of apples; and *Erysiphe cichoracearum*, powdery mildew of cucurbits and many other plants. On the other hand, *Microsphaera alni*, the cause of powdery mildew of lilac, seems to do little or no harm to its host even though it may occur on the same bush year after year.

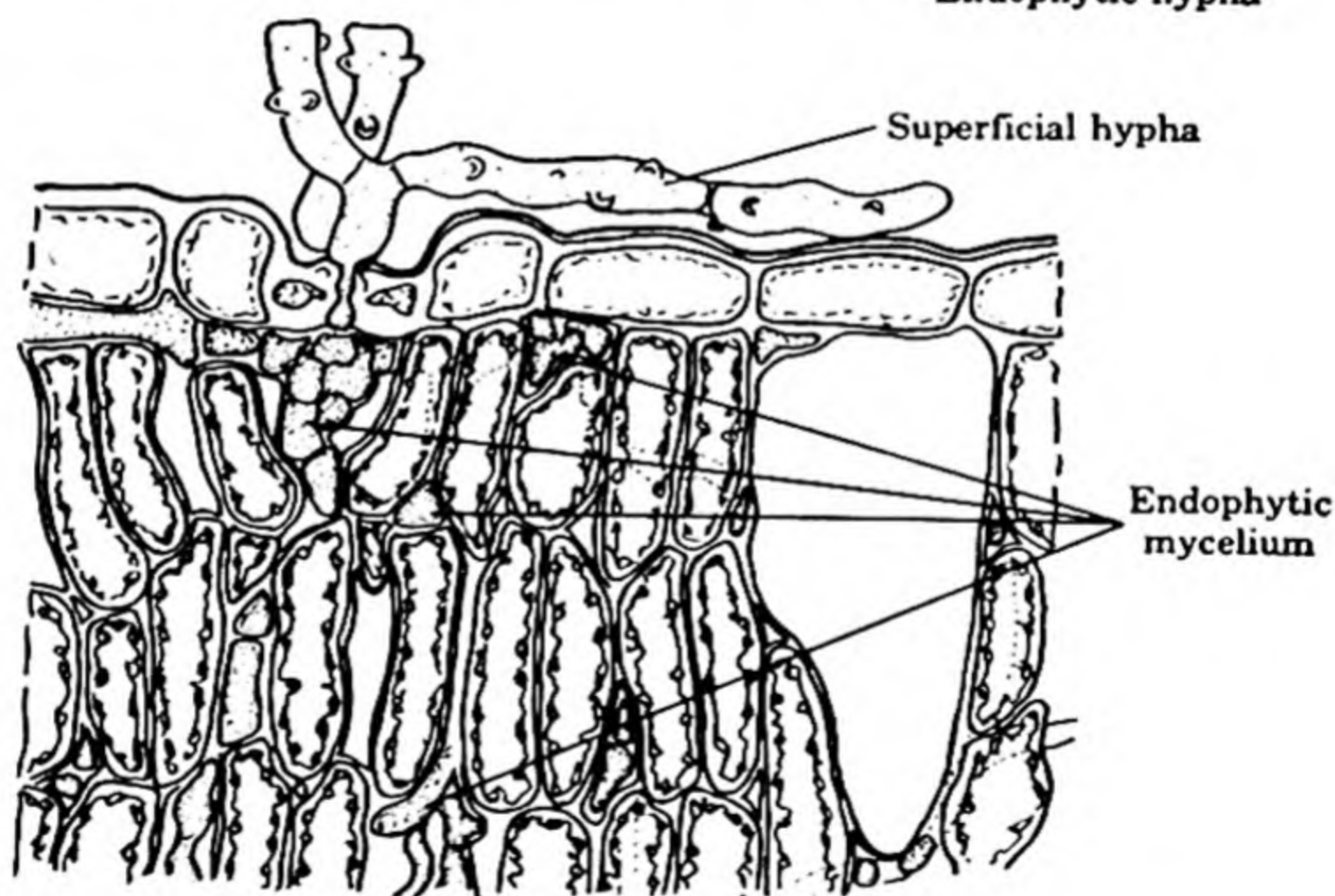
Somatic Structures. The mycelium of the Erysiphaceae is entirely superficial except for that of *Leveillula taurica* and *Phyllactinia corylea*. It consists of a network of colorless hyphae abundantly present on the epidermis of the infected parts of the host and securely anchored thereon by numerous haustoria which penetrate into the epidermal cells and obtain nourishment from their protoplasts (Figure 108A). In *Leveillula taurica*, a serious parasite of a number of host plants in the Mediterranean region, the hyphae pene-



A. *Erysiphe cichoracearum* D.C.



B. *Phyllactinia corylea* (Pers.) Karst.



C. *Leveillula taurica* (Lev.) Arnaud

Figure 108. Relationship between the host cells and the mycelium of certain Erysiphaceae. A, redrawn by permission from *Cryptogamic botany*, Vol. I, by G. M. Smith, 1938, McGraw-Hill Book Co., New York; B, C, redrawn from Arnaud, 1921, *Ann. épiphyt.*, 7:1-115.

trate into the leaf through the stomata and spread between the mesophyll cells (Figure 108C). In *Phyllactinia corylea*, a cosmopolitan parasite on over 100 host species, most of the hyphae are superficial, but these do not develop haustoria. The fungus obtains nourishment by special hyphal branches which enter the stomata, come in contact with the mesophyll cells, and send haustoria into them (Figure 108B).

As mentioned above, none of the Erysiphales has been grown in culture on artificial media. Culture work, however, has been successfully conducted on leaf discs on water or nutrient solutions in Petri dishes (Morrison, 1960/1961a). Some success also has been reported in growing *Erysiphe cichoracearum* on tumor tissue and on isolated epidermis and mesophyll tissue (Heim and Greis, 1953; Schnathorst, 1959b).

Asexual Reproduction. A few days after the fungus has infected the host, its somatic hyphae produce great numbers of long, hyaline, erect conidiophores. A generative cell in each conidiophore now begins producing conidia. In some species each newly formed conidium is abstricted before the next one matures. In other species the conidia cling together in chains (Figure 109B). In *Leveillula*, the mycelium of which is endophytic, the conidiophores grow out of the stomata and produce their conidia on the surface of the leaves. These conidiophores are often branched. In this genus, as well as in *Phyllactinia*, the conidia fall off as soon as they are formed, and no conidial chains are formed. This is true also of some species in other genera.

The conidia of the Erysiphaceae are hyaline and one-celled. They vary in shape from species to species, but in general may be described as ovoid or cylindrical with rounded edges. In *Phyllactinia* the conidia are described as clavate. The majority of powdery mildews have the same general type of conidial stage, which we recognize as the form-genus *Oidium* of the Deuteromycetes (see Chapter 18). Some authors separate the conidial stages of *Leveillula* and of *Phyllactinia* from the others by placing the former in the form-genus *Oidiopsis* and the latter in *Ovulariopsis*.

Professor C. E. Yarwood of the University of California, who has done a great deal of research on the powdery mildews, has shown that conidial physiology—formation, increase in size, abstriction, dissemination, germination—follows a diurnal cycle, certain processes taking place during the day, others at night (Yarwood, 1936, 1957).

Sexual Reproduction. In late summer, when conidial production slows down and eventually ceases, young cleistothecia begin to make

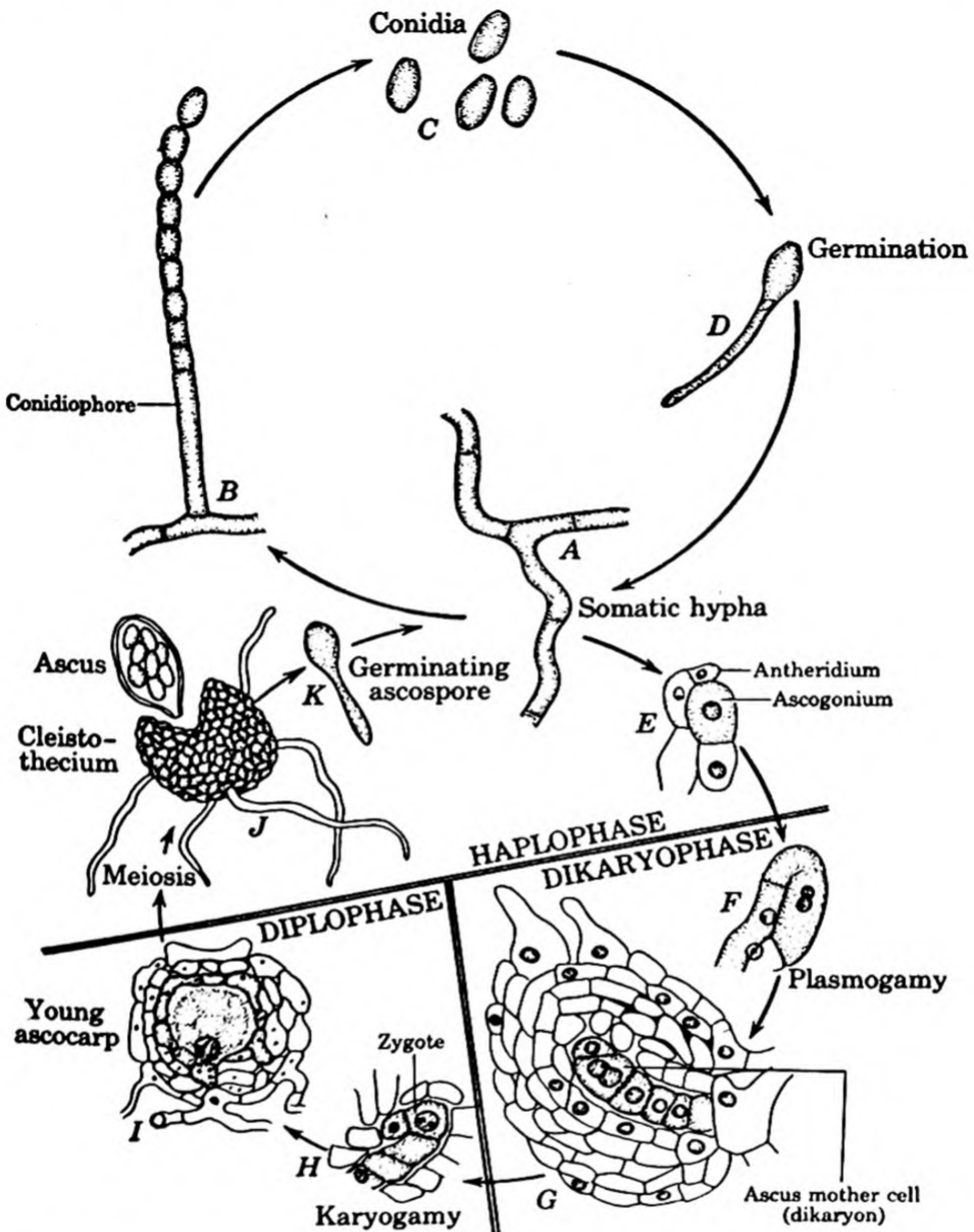


Figure 109. Life cycle of *Sphaerotheca castagnei*. B, redrawn from Salmon, 1900, *Mem. Torrey Bot. Club*, Vol. 9; D, K, constructed; E-H, redrawn from Harper, 1896, *Jahrb. wissen. Bot.*, 29:665-685; I, redrawn from Hein, 1927, *Bull. Torrey Bot. Club*, 54:383-417.

their appearance on the white mycelium. These are at first white, then orange, reddish, brown, and finally black when mature.

Several mycologists have investigated the sexual cycle in a number of the Erysiphaceae. Some species are homothallic, others heterothallic. The uninucleate gametangia arise from closely situated hyphae (Figure 109E). The antheridium is somewhat more slender than the ascogonium, and the two press closely together. Observers disagree as to the cytological details which follow, but it is probable that development takes place in accordance with the usual pattern. The antheridial nucleus passes into the ascogonium through a pore, but karyogamy is postponed until the ascus mother cell is formed (Bergman, 1941).

Cleistothecial formation and ascus development are long-drawn-out processes. In many species the asci mature late in the fall—October or November—and sometimes not until the following spring. Overwintering thus takes place in the cleistothecial stage, which is resistant to winter conditions, but there is strong evidence that in some perennial plants the mycelium of the powdery mildew may overwinter in the dormant buds of the host. Yarwood (1957) expresses the belief that the role of the ascus stage in the life cycle of the powdery mildews may have been overemphasized. In warm climates many species never form cleistothecia; they perpetuate themselves solely by means of conidia.

The mature cleistothecia of most Erysiphaceae are provided with characteristic appendages which vary considerably in length and character, and which, together with the number of asci developed in the cleistothecium, form the basis for generic separation (Figure 110). Cleistothecial appendages fall into four general types as follows: (1) mycelioid, which resemble somatic hyphae in being flaccid and indefinite, as in *Erysiphe*, *Sphaerotheca*, and *Leveillula*; (2) rigid, spear-like, with a bulbous base and pointed tip, as in *Phyllactinia*; (3) rigid with curled tips, as in *Uncinula*; and (4) rigid with dichotomously branched tips, as in *Microsphaera* and *Podosphaera*. Two genera, *Braziliomyces* and *Astomella*, possess no appendages. Neither of these occurs in North America.

The asci of the Erysiphaceae are globose to ovoid, and in many species have a short stalk. They are often fascicled and spread out like a fan when the cleistothecium is crushed and they are forced out. The asci have no pores but release the ascospores by bursting. The genera *Podosphaera* and *Sphaerotheca* produce only one large ascus in each cleistothecium. All other genera have more than one ascus in each ascocarp.

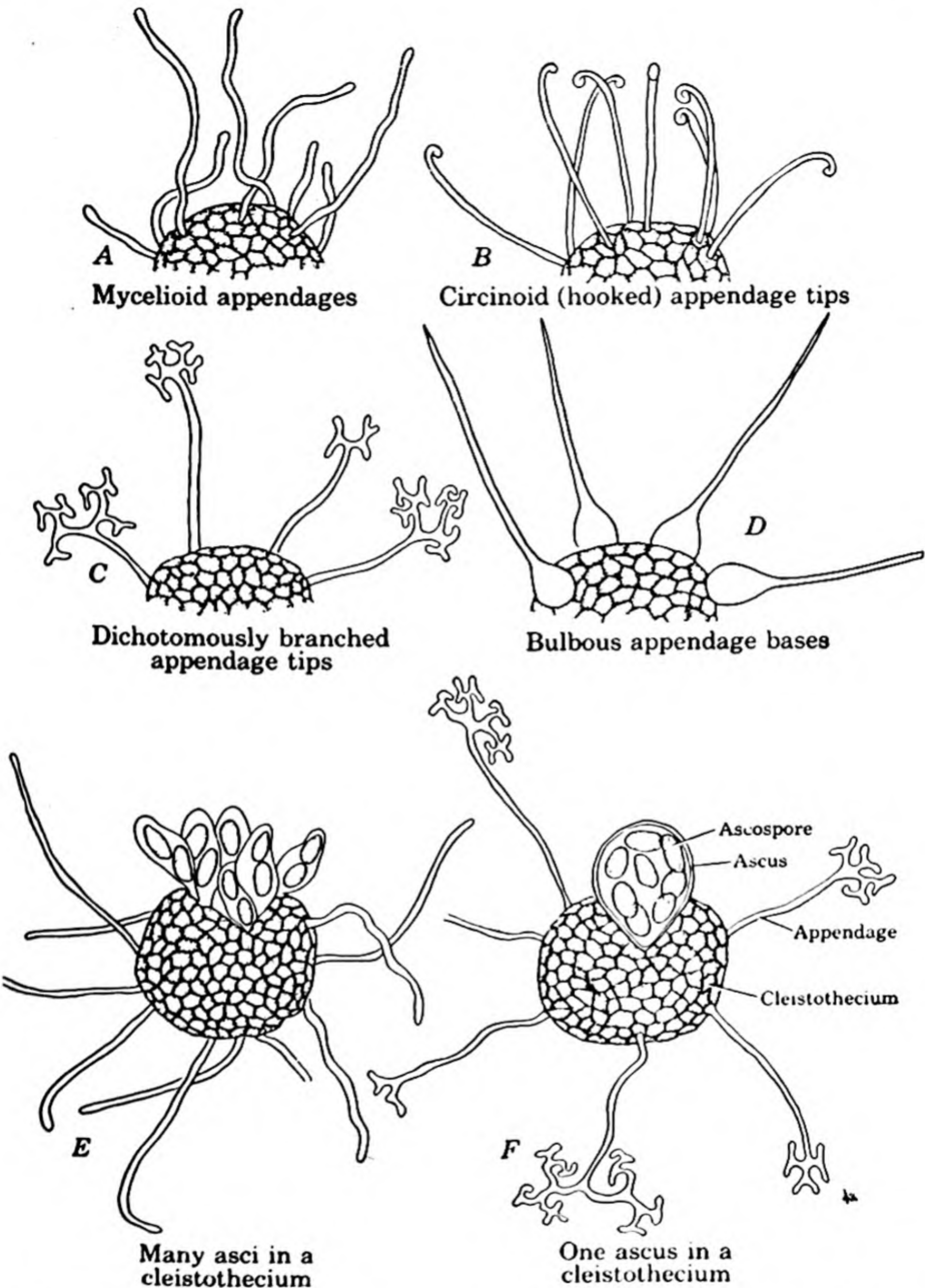


Figure 110. Taxonomic characteristics of the Erysiphaceae. A–D. Types of appendages. E, F. Variation in number of asci within a cleistothecium.

The ascospores are hyaline, except in *Astomella*. In all American species they are unicellular and oval. Four small genera are known, however, three with two-celled and one with four-celled ascospores. The number of ascospores in each ascus varies with the species and usually within the same species. For example, according to Salmon (1900), *Uncinula aceris* on maples regularly bears eight, rarely six, ascospores in each ascus, but *Erysiphe cichoracearum* has only two, rarely three, ascospores to the ascus. *Erysiphe polygoni* usually produces three to six ascospores to the ascus, but may have as few as two or as many as eight.

For an excellent, detailed discussion of the powdery mildews consult Yarwood's paper in *Botanical Review* (1957).

Classification. In 1900 Salmon listed forty-nine species of Erysiphaceae distributed among six genera. Since then the number of genera has more than doubled. Bessey (1950) recognized fourteen. Only six of these are found in North America. These may be recognized with ease in accordance with the characters employed in the following key:

SIMPLE KEY TO THE NORTH AMERICAN GENERA OF THE FAMILY ERYSIIPHACEAE

- | | |
|--|---------------------|
| A. One ascus to the cleistothecium | |
| B. Appendages mycelioid, indefinite | <i>Sphaerotheca</i> |
| BB. Appendages definite, their tips dichotomously branched | <i>Podosphaera</i> |
| AA. Several asci to the cleistothecium | |
| C. Appendages mycelioid, indefinite | <i>Erysiphe</i> |
| CC. Appendages definite, rigid | |
| D. Appendages with a bulbous base | <i>Phyllactinia</i> |
| DD. Appendages without a bulbous base | |
| E. Appendage tips dichotomously branched | <i>Microsphaera</i> |
| EE. Appendage tips coiled | <i>Uncinula</i> |

order MELIOLALES

Because the Meliolales resemble the Erysiphales in several respects, many authors group these two orders into one under the latter name. The differences, however, are at least as great as the resemblances, so that separation is probably justified.

The mycelium of the Meliolales is brown and mostly immersed in the substratum. The hyphae in most species bear characteristic

short protuberances, the **hyphopodia** (sing. **hyphopodium**; Gr. *hyphe* = web + *pous* = foot). The ascocarps are ostiolate and bear no appendages. The asci develop as a basal layer, whereas those of the Erysiphales, as noted previously, begin as an irregular layer in the middle of the ascocarp. The ascospores are brown and, in most species, multiseptate.

Martin (1961) recognizes two families, the Meliolaceae and the Englerulaceae. Both occur in tropical climates as obligate parasites of plants, the Meliolaceae being particularly abundant. Stevens (1927, 1928) published a good taxonomic monograph of the Meliolaceae which is indispensable for the identification of these fungi.

order CHAETOMIALES

The Chaetomiales are a relatively small order of saprobic Ascomycetes easily recognized by their characteristic perithecia, produced superficially without a stroma. The perithecia have a true ostiole which, in a few species, is greatly elongated, forming a long beak. Their most distinctive character, however, is the presence on the perithecium of numerous long hairs which give the order its name (Gr. *chaite* = long hair, mane). In many species the hairs covering the upper part of the perithecium are conspicuously curly (Figure 111). In the majority of species the asci, produced in basal tufts, are club-shaped, or broadly oval, but in some species they are cylindrical. They have thick, gelatinous walls which deliquesce before the spores mature. At maturity, the spores are embedded in jelly within the perithecial cavity and are often extruded in a **cirrus** (pl. **cirri**; L. *cirrus* = curl). This is a ribbon-like cylinder of spores, held together by mucus, and issuing from the ostiole much as tooth paste is squeezed out of a tube. The ascospores are generally dark and always unicellular. They vary in shape from species to species.

The order includes but a single family, the Chaetomiaceae, with three genera: *Chaetomium* with eighty-five species, *Ascotricha* with six, and *Lophotrichus* with three (Ames, 1961). Until recently the Chaetomiaceae were included in the order Sphaeriales. Martin (1961) elevated them to ordinal rank, recognizing that they do not fit well in any of the established orders.

Few species of *Chaetomium* produce conidia. In the other two genera, however, some species produce conidia profusely.

The Chaetomiaceae include a number of cellulose-destroying fungi which grow on paper and fabrics, sometimes causing considerable

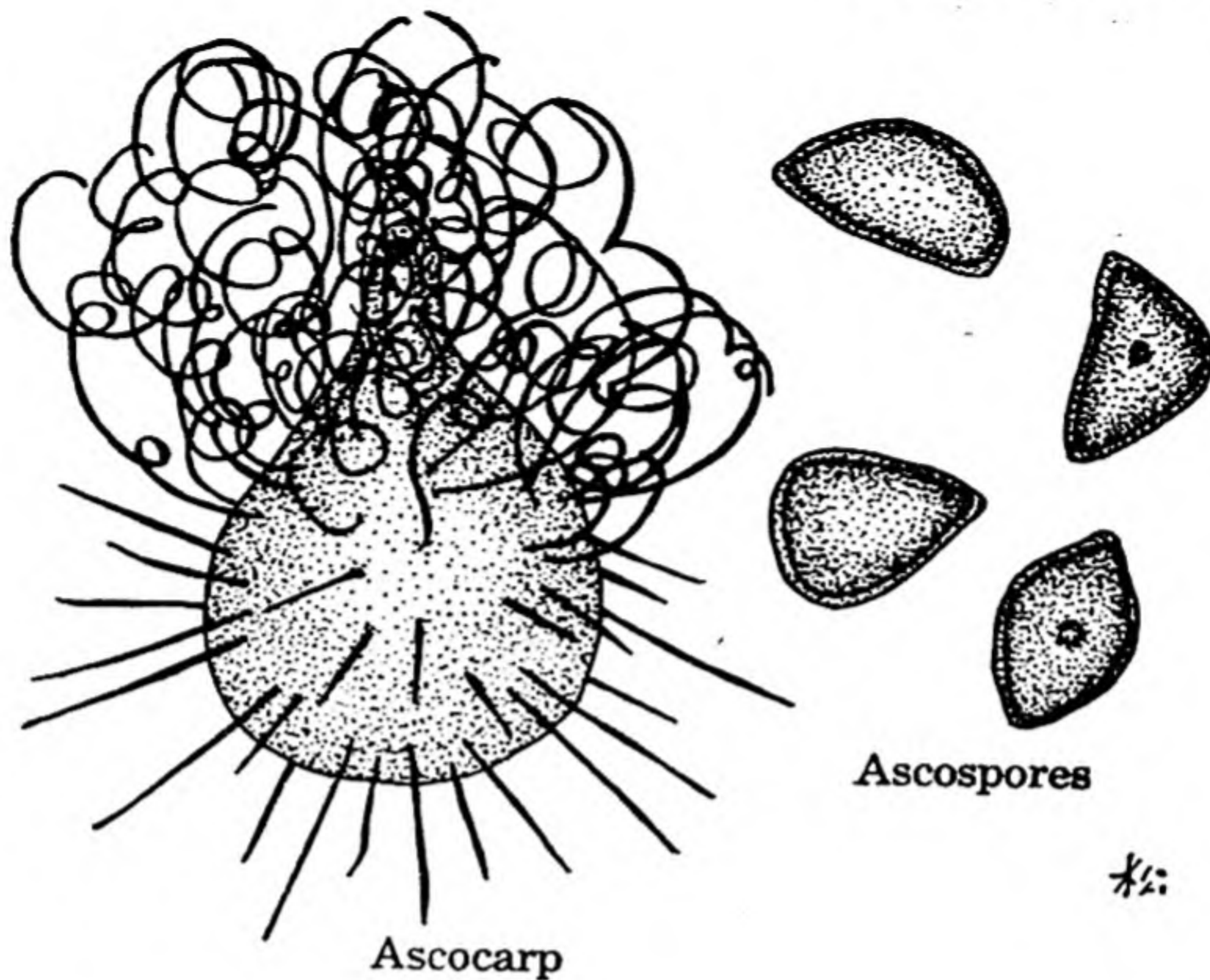


Figure 111. *Chaetomium* sp. The asci have disintegrated by the time the ascospores are mature.

damage. Some of the fungi which cause clothes to mildew belong to this family. Straw, dung, and similar materials are also common substrata for these fungi.

order SPHAERIALES

As limited here, the Sphaeriales include all Pyrenomycetes with dark, leathery or carbonous, globose or pear-shaped, ostiolate perithecia in which unitunicate asci, typically mingled with paraphyses, at least in the early stages of development, form a persistent hymenial layer or a basal tuft. The perithecia either are formed directly from the loose mycelial hyphae, or are associated with a well-developed stroma resting on top or sunken within it.

Occurrence, and Importance to Man. Many of the Sphaeriales are saprobic. We find them on decaying plant material such as logs and stumps, dead twigs and branches of trees, and dead leaves and stems of herbaceous plants. Others are normally coprophilous, inhabiting the dung of animals. Of the saprobic forms the pink bread-mold *Neurospora* can cause much trouble if permitted to establish itself in commercial bakeries. On the other hand, as we shall see pres-

ently, this same mold and some related genera are enormously important in the research laboratory as experimental organisms. In addition to the saprobes, the Sphaeriales include many parasitic fungi some of which cause serious diseases of plants. *Rosellinia necatrix* attacks the roots of grape vines, causing root rot; *Nummularia discreta* is the causal agent of nail head canker of apple trees; *Phyllachora graminis* parasitizes various grasses.

Somatic Structures. The mycelium of the Sphaeriales is typically ascomycetous, resembling that of many other orders of the same class. A few species, like *Rosellinia necatrix*, have a more or less characteristic mycelium, but with these few exceptions no species can be identified unless the fruiting bodies are available. Hyphae are generally composed of uninucleate or multinucleate, elongated cells.

Asexual Reproduction. Many Sphaeriales have lost their ability to produce conidia (assuming they ever possessed it), the ascospore stage being the only reproductive stage known. Some produce only microconidia which appear to function chiefly as spermatia in plasmogamy. Others produce large numbers of conidia. Past experience has taught that a great number of the so-called Fungi Imperfecti (Deuteromycetes) are genetically connected to the Sphaeriales, Diaporthales, or Hypocreales. Note here that in many genera of these orders there is no way to predict, by examining the ascigerous stage alone, the type of conidia that a given species will produce, for different species of the same genus frequently have very different conidial stages.

Sexual Reproduction. Mycologists have discovered antheridia and ascogonia in a number of Sphaeriales, but in some species the antheridia appear to have lost their function, the asci developing after the union of two ascogonial nuclei. *Neurospora sitophila* and *Podospora anserina* are examples of Sphaeriales which reproduce by spermatization. *Gelasinospora tetrasperma* does not produce male sex organs, plasmogamy taking place between somatic hyphae. The methods employed by the Sphaeriales for bringing together two compatible nuclei are therefore quite varied.

The Ascocarp. The ascocarp of the Sphaeriales is a typical perithecium which varies in shape from globose to pear-shaped or elongated, but is never disc- or boat-shaped. The ostiole is a conspicuous feature of the perithecium. It may be greatly elongated to form a long neck through which the ascospores must pass before they are liberated, or it may be a short papilla opening by a circular pore. Numerous variations between these two extremes are also found.

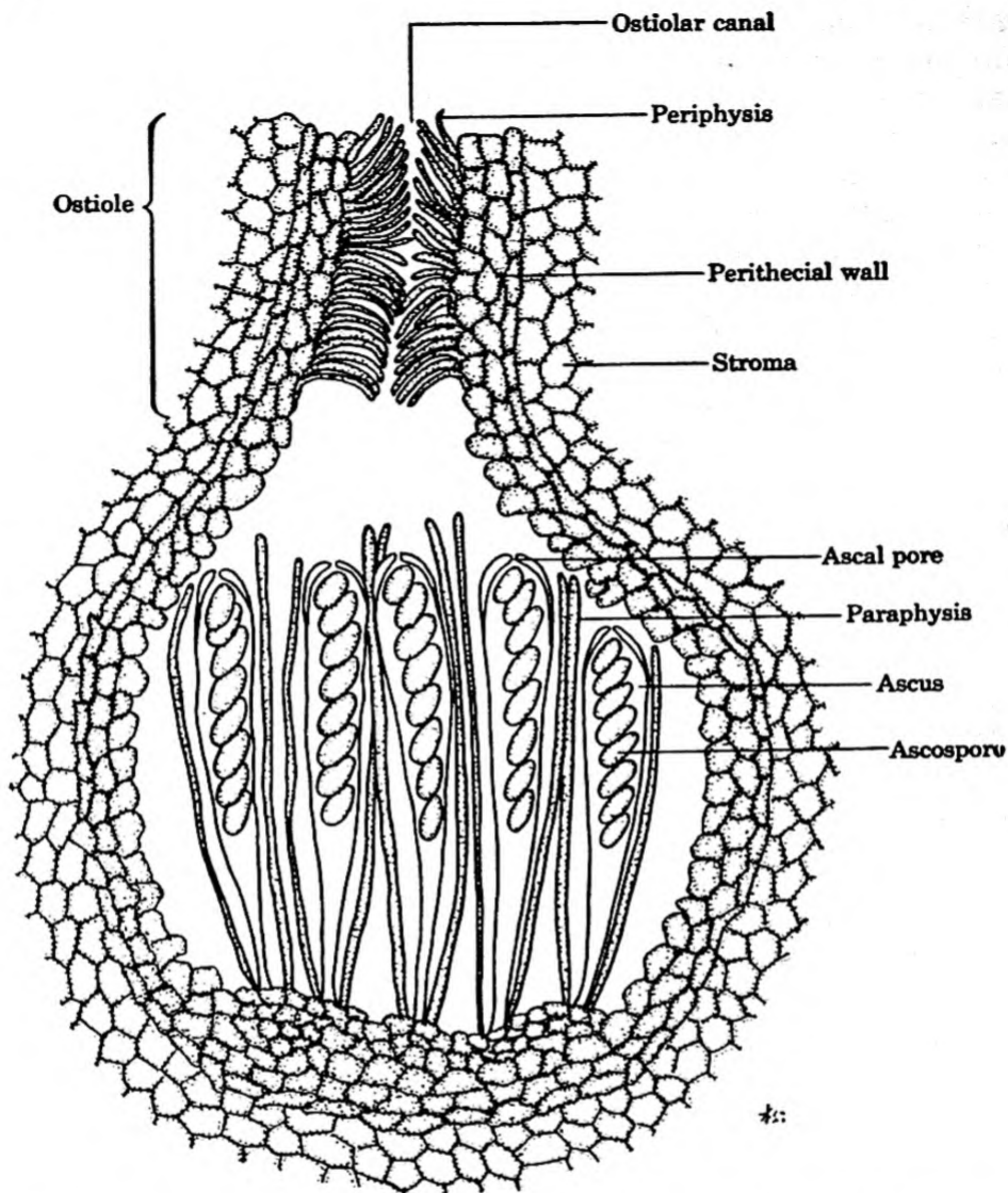


Figure 112. Diagram of an ascocarp showing the characteristics of the order Sphaeriales.

The ostiole is lined on the inside by the paraphyses, the presence of which is considered a sphaeriaceous *sine qua non*. The wall of the perithecium is definite, whether the latter is embedded in or lacks an easily discernible stroma (Figure 112).

The Asci. The asci of the Sphaeriales are club-shaped or cylindric. They open by a definite round, apical pore which is sometimes diffi-

cult to see. Their walls are thin and transparent except at or near the apex, where they are sometimes thickened, forming a short, narrow canal extending from the pore. The asci of the Sphaeriales mature at different times, so that ascospores of different ages can be found in the same ascocarp over a long period of time.

In many species paraphyses scattered among the asci are very numerous; in others there are few paraphyses; in still others no paraphyses whatsoever can be found in a mature perithecium. However, even in this last group paraphyses are probably present in the early stages of perithecial development but evanesce before the asci are fully formed, leaving no trace of their existence.

The Ascospores. The ascospores of the Sphaeriales vary considerably in shape, size, and color, although variation within the species is not so great. There are typically eight ascospores in each ascus, but some species produce only four. The ascospores are forcibly expelled from the perithecium when mature. The forceful expulsion of ascospores makes it easy to obtain pure cultures of these fungi by inverting a Petri dish containing sterile agar media over perithecial material and catching the ascospores on the surface of the agar as they are shot out of the ostiole.

Classification. At this stage of our knowledge, the division of the Sphaeriales into families and genera must be very tentative, for no two students of these fungi agree on the limits of this order or indeed on the chief characters which separate it from other pyrenomycetous orders. We shall recognize four families in accordance with the following key:

SIMPLE KEY TO THE FAMILIES OF THE ORDER SPHAERIALES

- | | |
|---|------------------------|
| A. Perithecia without an easily discernible stroma | |
| B. Perithecia superficial | <i>Sordariaceae</i> |
| BB. Perithecia immersed in the substratum | <i>Phyllachoraceae</i> |
| AA. Perithecia immersed in a stroma | |
| E. Stroma consisting of both host and fungal tissue | <i>Diatrypaceae</i> |
| EE. Stroma entirely fungal | <i>Xylariaceae</i> |

family SORDARIACEAE

From an economic standpoint, the Sordariaceae is not an important family as a whole, but the biologist should nevertheless be familiar with it because a number of organisms that belong here have proved of great value as experimental organisms. The most famous

of these is *Neurospora*, which has become the *Drosophila* of the fungus world.

The Sordariaceae are saprobes occurring on dung or on decaying plant parts. Their somewhat beaked, superficial, separate perithecia are dark brown or black, membranous or carbonous, and either glabrous or covered with soft hairs. The family is referred to as non-stromatic in the key, but there is some evidence that some species at least have a stromatic layer surrounding each perithecium, which can be peeled off by careful manipulation. The long, club-shaped or cylindric asci may be interspersed with paraphyses. However, in most species the paraphyses are evanescent before the spores mature so that in the mature perithecia no paraphyses are evident. The spores are dark brown to black and variously ornamented. Most species produce no conidia. Sexual reproduction varies considerably within the family, as will be shown in the brief discussion of four selected genera.

For taxonomic treatments of this family see Griffiths (1901), Griffiths and Seaver (1910), Cain (1934, 1950), Moreau (1953), Moreau and Moreau (1951), Cain and Groves (1948).

genus *SORDARIA*

The dark brown ascospores of *Sordaria* are surrounded by a gelatinous sheath. Sometimes this is thick and conspicuous. At other times it is difficult to detect.

Sordaria fimicola is the most common species and is the one that most investigators have studied. Doguet (1960), in an article on the nucleus of this species, states that during hyphal growth the nuclei divide by typical mitosis and that he has observed spindles 1.5–3 μ long oriented in various ways in the larger hyphae. This does not agree with the findings of Bakerspigel (1959a, b) on *Neurospora* and *Gelasinospora*, two other genera in this family.

Sordaria fimicola produces neither conidia nor microconidia. It reproduces solely by ascospores. *Sordaria fimicola* is homothallic. It has been studied experimentally by many students, and we have much information about its physiology and genetics. Curiously enough, the details of perithecial development have not been completely elucidated. Exactly how plasmogamy takes place is still not clear. Greis (1942) has reported gametangial contact between ascongonia and antheridia. Ritchie (1937) and Carr and Olive (1958) have demonstrated hyphal fusion between two strains and nuclear passage from one into the other. It is probable that somatogamy

operates as a sexual method instead of, or in addition to, gametangial contact.

The fungus produces perithecia sooner and more abundantly when the supply of carbohydrates is unfavorable for vegetative growth (Bretzloff, 1954). A pH above 6 is required for abundant fruiting. Biotin and, for some strains, thiamine are necessary for perithecial production. Biotin is a controlling factor not only in perithecial production but also in the formation and maturation of asci. At very low concentration of biotin perithecia without asci are formed. As the biotin supply increases, asci are formed, but the majority may be abortive. There is a direct correlation between available supply of biotin and percentage of mature ascospores produced (Barnett and Lilly, 1947).

Ingold and his associates (1953, 1955, 1956, 1957, 1960) have studied the discharge of the ascospores in many Ascomycetes. The perithecial necks in *Sordaria*, as in most members of the family, are positively phototropic. As the asci mature they swell and fill the upper part of the perithecium. One of the asci stretches and pushes through the ostiolar opening. Its base remains attached to the perithecial wall. As its tip protrudes, the ascus discharges all its spores explosively, collapses, and disintegrates, to be followed by other asci in succession. This method of ascospore discharge is probably not confined to *Sordaria*, but may be a pattern developed by several members of this family. After the ascospores are discharged, they germinate and produce mycelium which proceeds to develop perithecia when conditions are favorable.

Professor L. S. Olive of Columbia University, who has done much work on the cytology and genetics of homothallic fungi, has induced some interesting mutations in *Sordaria fimicola* which produce gray or yellow ascospores instead of the dark brown spores of the wild type. By growing the wild type together with the mutants he obtained some perithecia with heterokaryotic asci, *i.e.*, containing both wild type and mutant spores (Olive, 1956).

genus *PODOSPORA*

In *Podospora* the ascospores bear transparent, gelatinous appendages. *Podospora anserina*, a heterothallic fungus, produces four spores to the ascus. Each spore is formed around two of the eight nuclei developed in the ascus in such a way as to include one nucleus of each mating type. Such spores produce heterokaryotic mycelium which behaves like homothallic. This, of course, is secondary homothallism (see page 30). Occasionally ascospore devel-

opment is "abnormal" and five spores are produced in an ascus: three binucleate and two dwarf, uninucleate spores. The latter produce self-sterile mycelium. If the colonies formed from the two dwarf spores in the same ascus are mated, they complement each other and perithecia are produced (Ames, 1934).

Plasmogamy in this fungus is accomplished by spermatization. A spermatium coming in contact with a trichogyne of the opposite mating type empties its contents into it (Figure 17). Ascocarp development follows fertilization. If spermatization does not take place, the protoperithecia¹ do not develop further.

Much work of a similar type, but with the cytological details elucidated, has been done in Europe with *Bombardia lunata*, another of the Sordariaceae (Zickler, 1953).

genus *NEUROSPORA*

Neurospora sitophila, one of several known species of the genus *Neurospora*, is referred to commonly as the bakery mold or red bread-mold, because it frequently infests bakeries and causes considerable damage. When it invades the mycological or bacteriological laboratory as a contaminant, it plays havoc with cultures and is difficult to exterminate because of the enormous quantities of easily dispersed conidia that it produces, and because of its rapidly growing, creeping aerial hyphae. Two other common species are *Neurospora crassa* and *Neurospora tetrasperma*.

The mycelium of *Neurospora sitophila* consists of numerous, branched hyphae. Its aerial hyphae form a mass of mycelium easily recognized by the pink masses of oval conidia borne in chains on branched conidiophores. The fungus can propagate itself indefinitely by asexual means alone. Indeed, the conidial stage is the one usually found, as evidenced by the fact that the perithecial stage was not discovered until 1927, whereas the conidial stage has been known as *Monilia sitophila* since 1843.

Neurospora, like most members of the Sordariaceae, is a rapidly growing organism. The hyphal cells are multinucleate. The mycelium is pigmented, the amount of pigment varying with the substratum. A minimal medium of known chemical composition has been devised for growing the organism in culture with sucrose as the C source and KNO₃ as the N source. Inorganic salts, including

¹ A protoperithecium is a perithecial initial which will develop into a perithecium under proper conditions. Some mycologists use the term archicarp for such a structure.

the so-called trace elements, and biotin are included. The pH is adjusted to 6.5. This medium favors sexual reproduction (Wester-gaard and Mitchell, 1947).

As mentioned above, *Neurospora* produces multinucleate conidia abundantly. Uninucleate microconidia are also produced. Both are able to germinate and form mycelium.

Neurospora sitophila and *Neurospora crassa* are octosporous, hermaphroditic, and heterothallic. The female element is represented by the protoperithecia, in each of which a multinucleate as-cogonium is embedded (Backus, 1939). The ascogonia produce long hyphal branches which function as trichogynes (Figures 113F, F'). No antheridia are produced. The male elements are represented by microconidia produced in chains on microconidiophores (Figures 113A, A', H, H'), but almost any hyphal element, such as

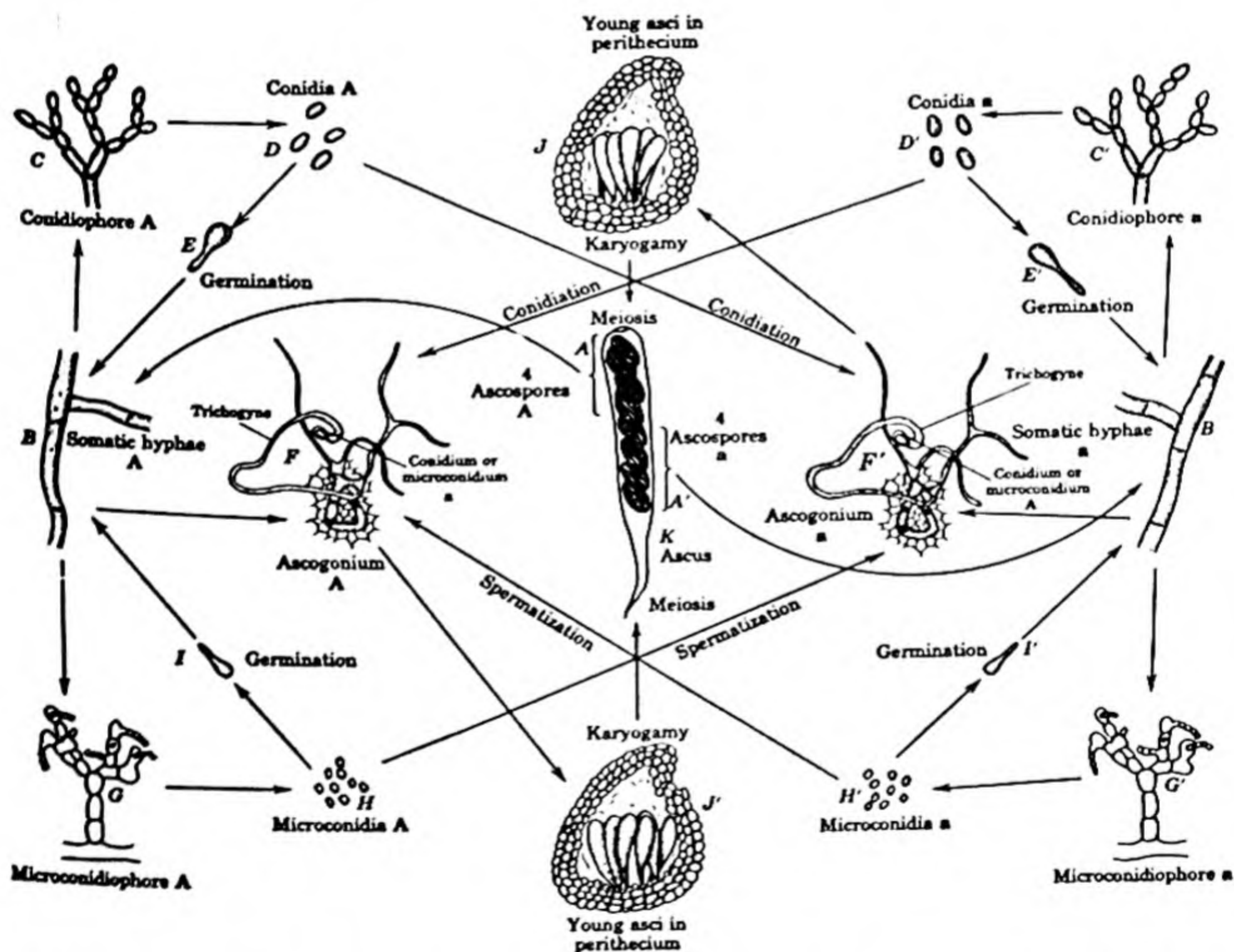


Figure 113. Life cycle of *Neurospora sitophila*. F, F', redrawn from Backus, 1939, *Bull. Torrey Bot. Club*, 66:63-76; G-I, G'-I', adapted from Dodge, 1932, *Bull. Torrey Bot. Club*, 59:347-360.

a conidium (Figures 113D, D') or a germ tube, can supply nuclei to the receptive trichogynes. Thus, in this species, we find the degeneration of the male sex organs and the delegation of the sexual function to less specialized parts of the thallus.

The cytology of ascus development has been worked out in detail by Miss McClintock (1945) and by Singleton (1953).

Mature perithecia are dark colored, pyriform, and beaked, and contain numerous octosporous asci, but no paraphyses at maturity (Figures 113J, J'). The spores are dark brown or black with ridges on the outer wall which characterize the genus *Neurospora* and give it its name. At first uninucleate, the ascospores finally contain two haploid sister nuclei. Four ascospores in each ascus are of one strain, and four are of the other (Figures 113K, A, A').

A great volume of literature has accumulated on the genetics and biochemistry of *Neurospora*, some of it based on *Neurospora sitophila* and *Neurospora tetrasperma*, but most of it on *Neurospora crassa*. *Neurospora tetrasperma* contains only four ascospores to the ascus, each ascospore containing two of the original eight ascus nuclei. Normal spores of this species germinate and produce self-fertile mycelium. A summary of much of what was known about *Neurospora* up to 1956 was published by Mme. Mireille Moreau-Froment. Her account includes an extensive bibliography.

genus *GELASINOSPORA*

We shall end our discussion of the Sordariaceae with a brief account of *Gelasinospora*, another genus about which we are acquiring considerable information.

As is true of all members of the family, *Gelasinospora* is a rapid grower. The cells of the mycelium are multinucleate. The nuclei migrate from cell to cell through the septa at a rather rapid rate (Dowding and Buller, 1940; Dowding and Bakerspigel, 1954). The mycelium is pigmented, the amount of pigment varying with the type of substratum. As is true of many other fungi, most species of *Gelasinospora* require biotin for growth and reproduction (Maniotis, 1960; Hackbarth and Collins, 1961).

Of the five or six known species, none produces conidia. Some, however, produce microconidia (Cain, 1950; Tylutki, 1958; Sloan and Wilson, 1958). Whether the microconidia are important in propagating the species is somewhat doubtful. In culture, they germinate with difficulty and grow slowly.

Sexual reproduction varies with the species. The details have

been investigated in only one or two forms. In the homothallic *Gelasinospora calospora*, plasmogamy takes place by the contact of an antheridium with a trichogyne (Ellis, 1960/1961). In the heterothallic variety *autosteira*¹ of the same species plasmogamy takes place by spermatization (Goos, 1959). In the secondarily homothallic *Gelasinospora tetrasperma* plasmogamy occurs by somatogamy (Dodge, 1935).

The ascocarp centrum is of the *Xylaria* type, as defined by Luttrell (1951), in that paraphyses are developed together with the ascogenous hyphae. The paraphyses, however, disintegrate by the time the ascospores mature (Meyer, 1957; Ellis, 1960/1961). As in some other genera of Ascomycetes the ascospores of *Gelasinospora* do not germinate easily as a rule. They need to be treated by heat, chemicals, or both to induce a high percentage of germination.

Olive and Fantini (1961) attempted to hybridize *Gelasinospora autosteira* with *Sordaria brevicolis*. Both are heterothallic. Abundant perithecia were formed at the line of contact between certain mating types, but no asci developed.

family PHYLLACHORACEAE

This family, formerly included in the Dothideales (Loculoascomycetidae), was transferred to the Sphaeriales by Miller (1949). The ascocarps are true perithecia sunken in the substratum. Even though it is here treated as a non-stromatic family, some species of *Phyllachora*, the only genus in the family, appear to form a stroma under certain conditions (Miller, 1954).

The perithecia are black, globose structures with a definite ostiole. These fungi chiefly inhabit leaves, forming their perithecia within the leaf tissues. The walls of the asci are uniformly thickened and have a large apical pore. There are many thread-like, apically free paraphyses in the hymenium. *Phyllachora graminis*, parasitic on grasses, is a well-known species.

family DIATRYPACEAE

The Diatrypaceae are stromatic Sphaeriales in which the stroma is composed of both host tissue and fungal elements. They are

¹ There is a difference of opinion concerning the status of this organism. Olive and Fantini (1961) believe it to be distinct from *Gelasinospora calospora* and return to its original designation as *Gelasinospora autosteira* (Alexopoulos and Sun, 1950).

chiefly saprobic, inhabiting dead bark or wood. The asci are club-shaped to cylindric with a long, tapering, persistent stalk and form a definite hymenial layer in the perithecium. Paraphyses are formed but gelatinize by the time the perithecium is mature. The ascospores are usually sausage-shaped, hence the name *Allantosphaeriaceae*, which has often been used for this family. They are one-to many-celled, yellowish individually and brown in mass. Wehmeyer (1926) discusses the family in detail. —

family XYLARIACEAE

As defined by Luttrell (1951), the Xylariaceae are characterized by distinctive asci, which bear a crown at the apex, numerous persistent paraphyses, and dark-colored, inequilateral ascospores. Some stromatic genera, previously included in the Sordariaceae, should be transferred to the Xylariaceae, as suggested by Moreau (1953). As treated here, most Xylariaceae have well-developed stromata. The importance of this character in delimiting families may be de-emphasized as we learn more about the structure of the ascus and the development of the perithecial centrum.

The stromata of the Xylariaceae are composed entirely of fungal tissue in which perithecia with definite walls are embedded, with their necks slightly protruding. The stromata are cushion-shaped as in *Hypoxylon* and *Daldinia*, club-shaped as in *Xylaria* (Figure 114) or more or less cup-shaped as in *Nummularia*. Most of the



Figure 114. *Xylaria polymorpha*. Photograph by Philip G. Coleman.

Xylariaceae are saprobes, but a few, like *Hypoxylon pruinosum* and *Nummularia discreta*, are parasitic. The latter causes nail head or Illinois canker of apple trees.

order DIAPORTHALES

In the Diaporthales the asci have short evanescent stalks soluble in water. The gelatinization of the stalks results in the release of the asci within the perithecium and their eventual escape en masse through the ostiole. The ascal tips are thickened, forming a narrow canal in the center through which the ascospores pass while being discharged.

The perithecial centrum is at first pseudoparenchymatous, but the pseudoparenchyma is destroyed as the asci and paraphyses grow. There are usually no paraphyses in the mature perithecia, these having gelatinized before the ascocarp completes its development.

The order is variously subdivided into families. We shall discuss only the Gnomoniaceae and the Diaporthaceae. The presence of a well-developed stroma in the Diaporthaceae, as opposed to the absence of an easily discernible stroma in the Gnomoniaceae, serves as the major characteristic separating these groups. There is little doubt of the relationship of these two families. Wehmeyer (1926) considers the Diaporthaceae to be derived through three lines of development from the Gnomoniaceae, and Miller (1949) actually transfers most genera of the Gnomoniaceae to the Diaporthaceae, and considers the Gnomoniaceae no longer valid.

family GNOMONIACEAE

The perithecia of the Gnomoniaceae are buried in the substratum, but each of them is provided with a prominent beak which protrudes from the surface and serves as an exit for the asci and ascospores.

Among the most important species, from an economic standpoint, are *Gnomonia leptostyla*, the cause of anthracnose of walnut and related hosts; *Gnomonia veneta*, the cause of sycamore anthracnose; *Gnomonia ulmea*, the cause of leaf spot of elm (Figure 115); and *Gnomonia erythrostoma*, the cause of cherry leaf scorch. The conidia of most species of this family are produced in acervuli; an exception is *Gnomonia fragariae* on strawberry, which bears its conidia in pycnidia.

Three papers by Morgan-Jones (1953, 1958, 1959) on ascocarp

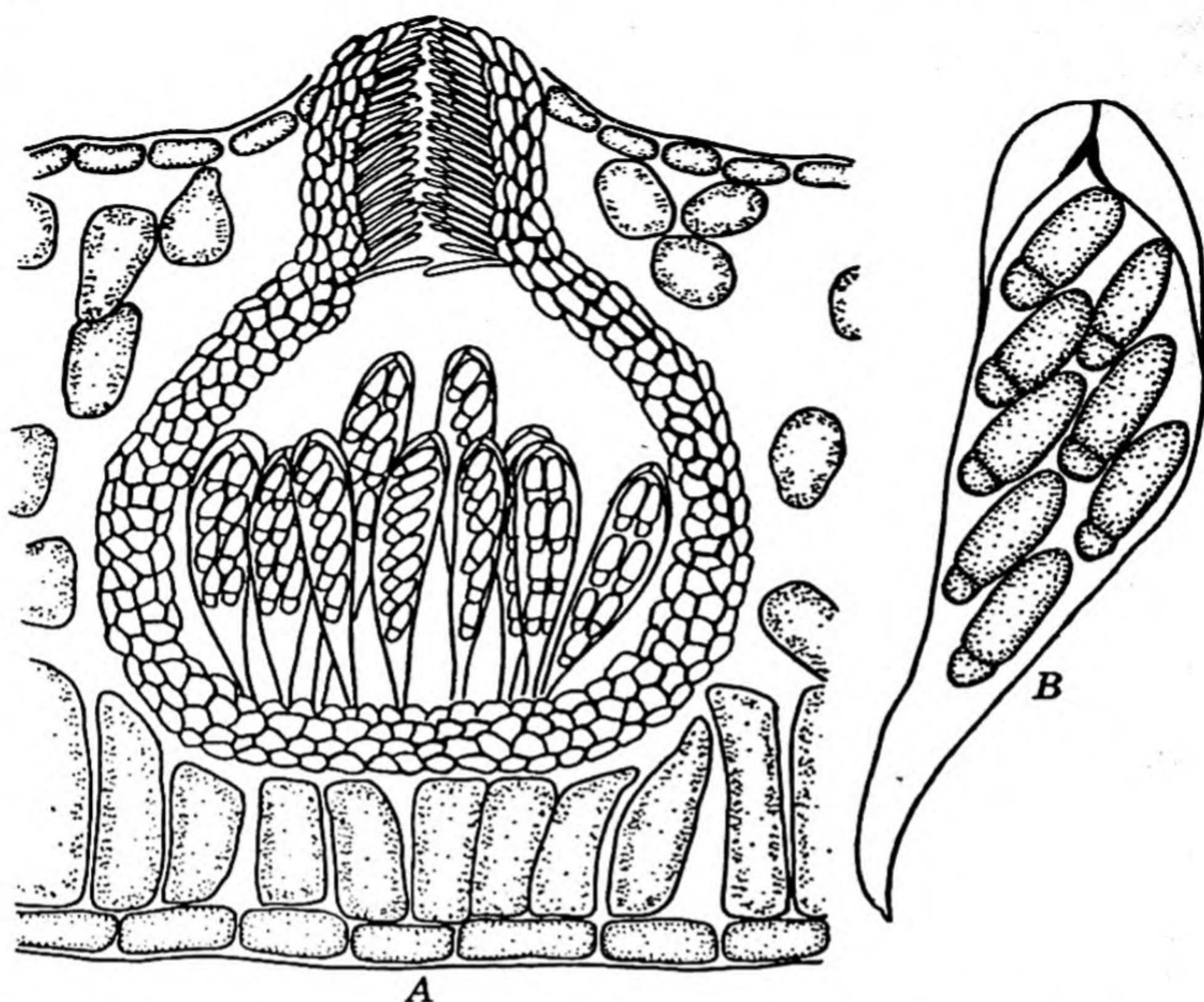


Figure 115. *Gnomonia ulmea*. A. Perithecium embedded in the host tissue (longitudinal section). B. Ascus with ascospores. Note thickened ascial apex.

development in *Gnomonia* are of particular interest. This investigator finds that, in five species he studied, a central pseudoparenchyma develops, as might be expected, but true ascogenous hyphae are lacking and the asci develop from a system of ascogenous cells which proliferate independently. You may recall that this situation exists also in *Ceratocystis*, and Morgan-Jones points out the similarity in this respect between the two groups.

family DIAPORTHACEAE

The Diaporthaceae form their perithecia immersed in a stroma with only their long beaks protruding. The largest genus in this family is *Diaporthe*. The ascospores are hyaline and two-celled. In this genus we find a direct correlation between ascigerous and conidial stages. The imperfect stages of *Diaporthe* species all be-

long to the form-genus *Phomopsis* (see page 402). Among the economically important species are the following: *Diaporthe citri* is the cause of citrus melanose, *Diaporthe vexans* causes a serious fruit rot of eggplant, and *Diaporthe phaseolorum* and its two varieties attack lima beans, soybeans, and other plants.

Endothia, another genus in the Diaporthaceae, produces its perithecia deeply buried in a stroma, their long necks terminating at the surface in an ostiole. The asci are club-shaped; there are no paraphyses. The ascospores are one or two-celled, hyaline to pale yellow. They vary in shape from almost ovoid to sausage-shaped.

Endothia parasitica is the cause of chestnut blight. Introduced into North America from eastern Asia at the beginning of the century, it ravaged the chestnut forests and exterminated the American chestnut. It has now been introduced into Europe, where it threatens the European chestnut. The conidial stage of this fungus is in the form-genus *Cytospora*. The curved conidia are extremely minute. They issue from the pycnidia in cirrhi, usually referred to as spore horns.

Glomerella produces its perithecia either in groups in a stroma or separately. The stroma may not be well developed or may be lacking. The perithecia are beaked. The ascospores are hyaline, one-celled, and curved. *Glomerella cingulata* is the cause of bitter rot of apples and of anthracnose of a large number of other plants (Shear and Wood, 1913). *Glomerella lindemuthiana* causes bean anthracnose. In this genus we find again a good correlation between ascigerous and conidial stages (see page 405). All species of *Glomerella* have the same type of imperfect stage (*Gloeosporium* or *Colletotrichum*) producing hyaline, ovoid, cylindrical, or somewhat dumbbell-shaped conidia in acervuli. The acervuli sometimes bear bristles called setae (sing. seta; L. seta = bristle), but this character seems to be determined, at least partially, by the environment.

Glomerella cingulata has been studied extensively, particularly at Louisiana State University. Dr. C. W. Edgerton first reported this fungus as being heterothallic in 1914.

The perithecium arises from two uninucleate mycelial branches which develop into an inner and an outer coil (McGahen and Wheeler, 1951). The outer coil develops into a peridium. The inner coil is the ascogonium. The whole structure is a protoperithecium which develops into a perithecium after plasmogamy. When conidia of the opposite mating type germinate close to a protoperithecium, a conidial germ tube grows toward it, enters, and applies itself onto the ascogonial coil, which up to this time consists

of uninucleate cells. The walls between the two dissolve and plasmogamy occurs. One or more of the ascogonial cells becomes binucleate, but only one, probably the tip cell, gives rise to the ascogenous hyphae which develop asci from croziers. There are a number of variations of this pattern, particularly in regard to the method by which plasmogamy is accomplished. Sexuality in *Glomerella* is extremely complex, and the genetic literature on this organism has grown considerably. A few of the papers dealing with this subject are listed at the end of the chapter.

order HYPOCREALES

The Hypocreales are a large and probably heterogeneous order, as now constituted, in which we generally place fungi which have a bright-colored, ostiolate perithecium with relatively soft or waxy walls, or bright-colored, more or less soft stromata bearing perithecia either on the surface or immersed in the stromatic tissues. Although it is generally agreed that color and consistency of the ascocarp wall are not good taxonomic criteria, so few species have been investigated from the developmental and cytological angles that it seems best to retain the old concept until we have something better to substitute for it.

Both Miller (1949) and Luttrell (1951) believe that we may be able to define this order on the basis of the *Nectria* type centrum which has been found in a number of species. The characters of this type of centrum are the following: a true perithecium¹ with a wall of its own, with an ostiole lined with periphyses; clavate or cylindric asci lining the base and sides of the inner wall of the perithecium and growing among pseudoparaphyses; absence of basal paraphyses. Pseudoparaphyses (sing. pseudoparaphysis; Gr. *pseudo* = false + *paraphyses*) are sterile threads which originate at the roof of the ascocarp cavity, grow downward, and become attached to the floor of the cavity.

Munk's statement (1954b) that he found this type of centrum in twelve species of *Nectria* certainly reinforces the idea of delimiting the Hypocreales on this basis, but many more species in different genera must be investigated before we have a clear picture of the situation. In this connection we should mention that Munk does not subscribe to the idea that the sterile structures in the *Nectria* centrum are homologous to the pseudoparaphyses of the Loculoascomycetidae (see page 365). He calls them apical paraphyses in

¹ See Strikmann and Chadefaud (1961) for a different interpretation.

Nectria because they originate from an area just below the periphyses and grow downward (Munk, 1954a).

Strikmann and Chadeffaud (1961), after a lengthy discussion of the *Nectria*-type ascus and ascocarp, consider the Hypocreales (*Nectriales*) to be a key group in the evolution of the Ascomycetes.

The Hypocreales, as we shall delimit them here, include a number of species parasitic on green plants, fungi, or insects, and also a large number which are saprobic. A few of the parasitic species grow on the fruiting bodies of various Basidiomycetes. Without reference to parasitism, the order is often subdivided into two large families, the Nectriaceae and the Hypocreaceae. To these we shall add the Hypomycetaceae and the Melanosporaceae.

So large and so varied is this order that any attempt to typify it by the description of one or two species is misleading. We shall discuss the life history of *Nectria cinnabarina*, so far as it is known, as a representative of the genus *Nectria*, which is one of the most common genera of the Hypocreales, and we shall confine our discussion of the other families to a brief statement.

family NECTRIACEAE

The Nectriaceae include species which produce their perithecia superficially, either on a well-developed stroma or without a stroma. The stroma, when present consists of short cells (Munk, 1957). The centrum in most species which have been carefully investigated is of the *Nectria* type, but there are some exceptions.

genus NECTRIA

The genus *Nectria*, to which some important parasites of trees belong, is one of the larger genera in this family. *Nectria galligena*, *Nectria cinnabarina*, *Nectria ditissima*, and *Nectria coccinea* are the most common species in the genus. Of these, the first is the most serious parasite. It attacks fruit trees as well as shade trees and is widely distributed in Europe and North America. It causes the so-called European canker disease of a large number of hardwood trees. *Nectria cinnabarina*, so called because of the cinnabar color of its fruiting bodies, attacks primarily shade trees. It is considered a weak parasite, entering the host only through wounds, and causes relatively little damage as compared with *Nectria galligena*. It appears, however, to be even more widely distributed than the latter. *Nectria haematococca* is the cause of the serious wilt disease of peas and probably of a large number of other plants.

The genus *Nectria* is characterized by a perfect stage which produces its perithecia on the surface of a cushion-shaped stroma. The ascocarps are brightly colored. The ascospores are generally two-celled, hyaline, and often boat-shaped. Different species have different imperfect stages which in themselves do not appear to be related, but which, nevertheless, belong to perfect stages which resemble one another. Thus, *Nectria galligena* produces large crescent-shaped, multiseptate conidia of the *Fusarium* type (see page 417), as does *Nectria haematococca*, whereas *Nectria cinnabarina* produces minute, one-celled conidia of the *Tubercularia* type (see page 417). In contrast, therefore, to such genera as *Eurotium* and *Diaporthe*, and the various Erysiphaceae in which there is a direct correlation between perfect and imperfect stages, in the genus *Nectria* as delimited today no such correlation exists. Nevertheless, the fact that several species of the Hypocreales, distributed over several genera, all have a *Fusarium* type of imperfect stage points to a definite genetic connection between *Fusarium* and the hypocreaceous gene complex.

Nectria cinnabarina Fr.

Nectria cinnabarina attacks the trunk, branches, and twigs of susceptible hosts, chief among which is the maple. The mycelium attacks and destroys the sapwood of the tree, causing the bark to die of desiccation (Boyce, 1948). A canker thus develops in older limbs. Young twigs die when attacked; this form of the disease is known as die-back.

After the mycelium has made considerable growth, the asexual reproductive phase of the organism develops and becomes evident in the form of bright, orange-pink sporodochia (sing. sporodochium; Gr. *sporos* = seed, spore + *docheion* = container) which appear on the surface of the bark over the infected area. Sporodochia (Figures 116B, C) are cushion-shaped stromata which develop under the surface, but become erumpent at maturity. At first they appear as small velvety cushions, whitish or pink. Soon they enlarge and turn orange-pink. At maturity, they are provided with a short stalk, and in longitudinal section under the microscope appear mushroom-shaped. The surface layer of the sporodochium consists of innumerable simple or sparingly branched conidiophores, on the tips of which elongated-oval conidia are borne (Figures 116D, E). The fungus reproduces during the growing season by means of conidia produced in vast numbers, which are distributed by the wind, germinate, and initiate new infections.

As the season progresses, small dark red perithecia (Figure 116F) begin to form superficially at the base of the stromata that have borne the conidiophores earlier. New ascocarps are formed progressively from the base of the stroma to the top until the entire stroma is cov-

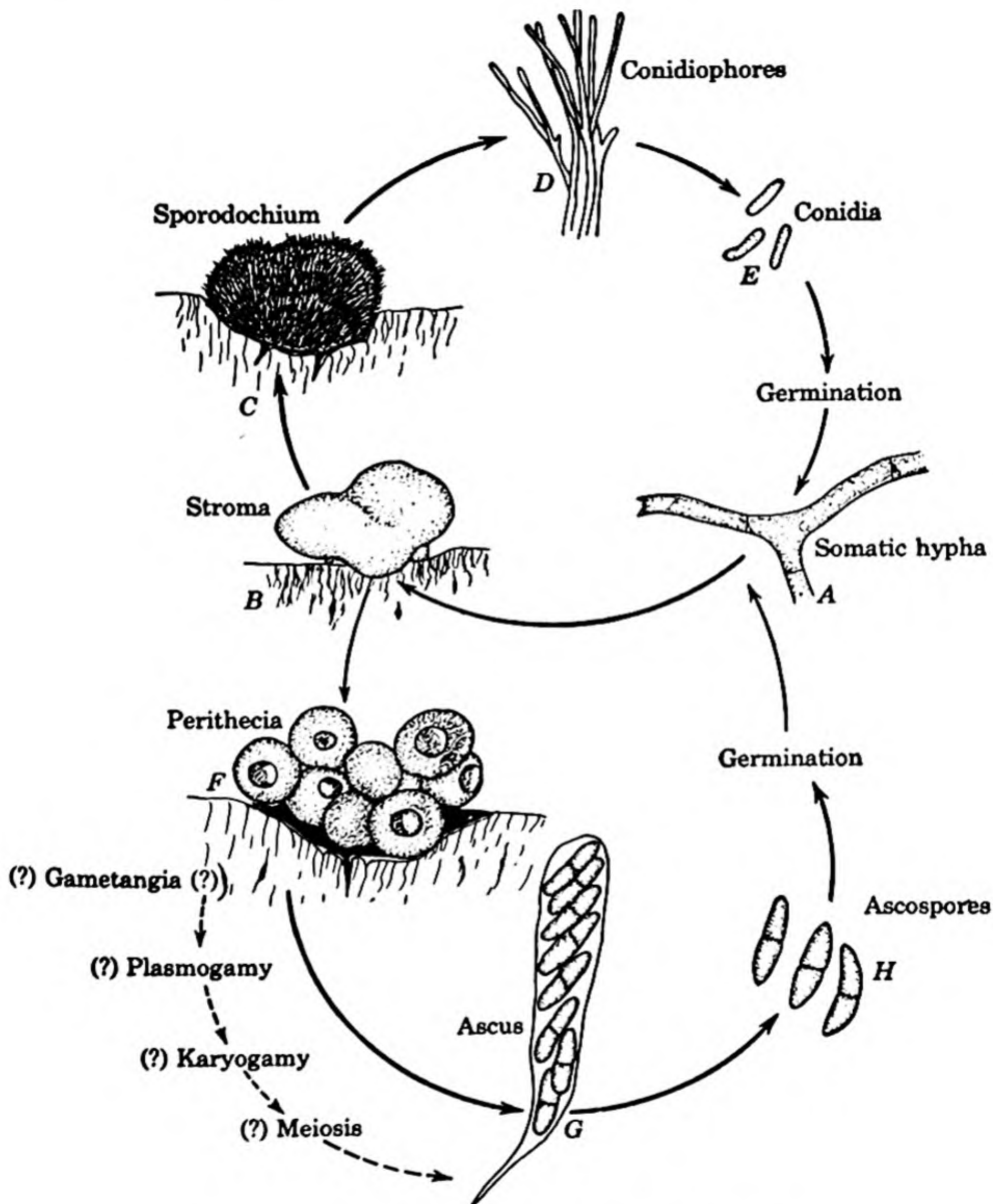


Figure 116. Life cycle of *Nectria cinnabarina*.

ered with crowded perithecia which have eventually replaced the conidiophores. Thus the same stroma (Figure 116B) which, during the growing season, supported the imperfect stage later forms the base for the perfect stage. The perithecia of *Nectria cinnabarina* are ostiolate. They contain numerous club-shaped asci arising from the basal wall of the perithecium, and growing among pseudoparaphyses. Each ascus (Figure 116G) contains eight two-celled, boat-shaped ascospores which, upon release from the perithecia, germinate and form mycelium. This normally takes place in the spring, after the fungus has passed the winter in the perithecial stage. Cytological details are lacking for this species. In *Nectria galligena* ascogonia and microconidia (spermatia ?) were found by Miss Cayley (1921), but their function has not been determined. In a study of *Nectria flava*, Gilles (1948) reported that the development of the ascogonium takes place in the absence of plasmogamy, the fungus developing no male organs. The ascus, in this species, develops from a terminal binucleate cell of an ascogenous hypha without crozier formation.

Before we leave this family we should mention the genus *Gibberella*. Several species are known. *Gibberella zeae* (= *Fusarium graminearum*) causes corn red ear-rot. *Gibberella fujikuroi* (= *Fusarium moniliforme*), the cause of a serious rice disease in the Orient, and of pink ear-rot of corn in the United States and elsewhere, is the source of gibberellic acid, which is being used extensively as a growth-promoting substance.

family HYPOCREACEAE

The Hypocreaceae are stromatic with their perithecia immersed completely in a stroma consisting of hyphal elements. The perithecial centrum, as far as is known, is similar to that of the Nectriaceae. Some authors (Luttrell, 1951; Martin, 1961) combine the two families, but Munk (1957) believes that the structure of the stroma is an important and distinct enough character to separate the two. He removes, however, the genus *Hypomyces* from this family and erects the family Hypomycetaceae to accommodate it.

Hypocrea is the most typical genus. The asci in *Hypocrea* are narrowly cylindrical, containing eight two-celled spores in one series. The spores are constricted at the septum and break so that the ascus at maturity appears to have sixteen spores. *Hypocrea sulfurea* is often encountered. It grows and sporulates easily in agar culture. Of interest is the genus *Chromocrea*, which develops a green pigment in the spores and in the cells around the ostiole of

the perithecium. In *Chromocrea spinulosa* each ascus contains four large and four small two-celled spores. As in *Hypocrea*, these break into their component cells so that the mature ascus actually contains eight spores of each size. The small spores produce sterile colonies. The large spores produce colonies which form fertile ascocarps with asci containing both types of spores in the expected ratios and arrangement. Mathieson (1952) concludes that the fungus is heterothallic and that the mating type gene of the large spores mutates to the other mating type, resulting in heterokaryotic asci.

family HYPOMYCETACEAE

This family was erected by Munk (1957) for the genus *Hypomyces*, which is usually included in the Hypocreaceae. The genus is, however, distinct both in its type of centrum and in the morphology of its ascus. The perithecia are formed in a felt-like mat called a **subiculum** (pl. **subicula**; L. dimin. of *subex* = underlayer). The perithecial centrum is pseudoparenchymatous and lacks sterile threads. The long, cylindrical asci are thickened at the apex, which is perforated by a narrow, cylindrical pore. Luttrell (1951) places *Hypomyces* in the Melanosporaceae, which he includes in the Diaporthales. Most species of *Hypomyces* are parasitic on mushrooms.

family MELANOSPORACEAE

In *Melanospora*, the typical genus of this family, the perithecia are mostly light colored, soft, and often very transparent. In many species the asci dissolve easily and liberate the spores within the perithecial cavity. The ascospores are then liberated in a cirrhous from the perithecial beak, which, in most species, is very long.

What genera should be included in this family has not been settled. In addition to *Melanospora*, some authors include *Neurospora*, *Gelasinospora*, and some other genera I have placed in the Sordariaceae.

Doguet (1955) has given us an excellent monograph on *Melanospora*.

order CLAVICIPITALES

The Clavicipitales produce their perithecia within a well-developed stroma composed entirely of fungal tissue. Each of the long, narrowly cylindrical asci has a thick cap perforated by a long, cylindrical pore through which the ascospores escape (Ingold, 1953). Paraphyses are formed on the lateral walls of the perithecium, but

not among the tufted asci at the base. The ascospores are thread-like and in many species break into fragments after they are released, each fragment behaving as a spore.

All species in this order are grouped in the single family Clavicipitaceae which some authors (Bessey, 1950; Martin, 1961) classify in the Hypocreales and others (Miller, 1949; Luttrell, 1951) in the Sphaeriales (Xylariales). In recognizing the order Clavicipitales I am following Nannfeldt (1932), Gäumann (1952), and Dennis (1960). Representative genera of the Clavicipitaceae are *Claviceps*, parasitic on grasses, and *Cordyceps*, parasitic on insects, spiders, and on the fruiting bodies of some fungi.

family CLAVICIPITACEAE

Claviceps purpurea (Fr.) Tul.

Claviceps purpurea, the cause of ergot of rye, will be used as an example of the family Clavicipitaceae. The thread-like ascospores are forcibly discharged from the perithecia in the spring about the time that certain susceptible grasses, such as rye, are in bloom. If the ascospores, which are wind-disseminated, happen to reach the flowers of the rye plant or other susceptible host, they germinate (Figure 117L), send germ tubes into the ovary, and cause infection. As the mycelium develops, it destroys the ovary tissues and replaces them in the flower by a soft, white, cottony, mycelial mat which soon becomes covered by acervulus-like layers of short conidiophores bearing minute, oval conidia at their tips (Figure 117B). These conidia are mixed with a sticky, sweet, nectar-like secretion, the origin of which is obscure. Attracted by this nectar, insects visit the infected ovaries and distribute the conidia to uninfected flowers, spreading the fungus in this way.

In the meantime, the mycelial mat, which has produced the conidiophores, continues to develop, begins to harden, and is eventually transformed into a hard pink or purplish, pseudoparenchymatous sclerotium. In shape the sclerotium resembles the grain of rye whose position it occupies, but it exceeds the rye grain in length. This sclerotium is the "ergot" of commerce. Thus, the mature heads of rye bear sclerotia of *Claviceps purpurea* together with rye grains on their spikelets (Figure 117E), the uninfected ovaries developing normally, the infected ones being destroyed and replaced by the sclerotia of the fungus as described. During the harvesting operations, many of the sclerotia are knocked off the spikelets, and fall to the ground,

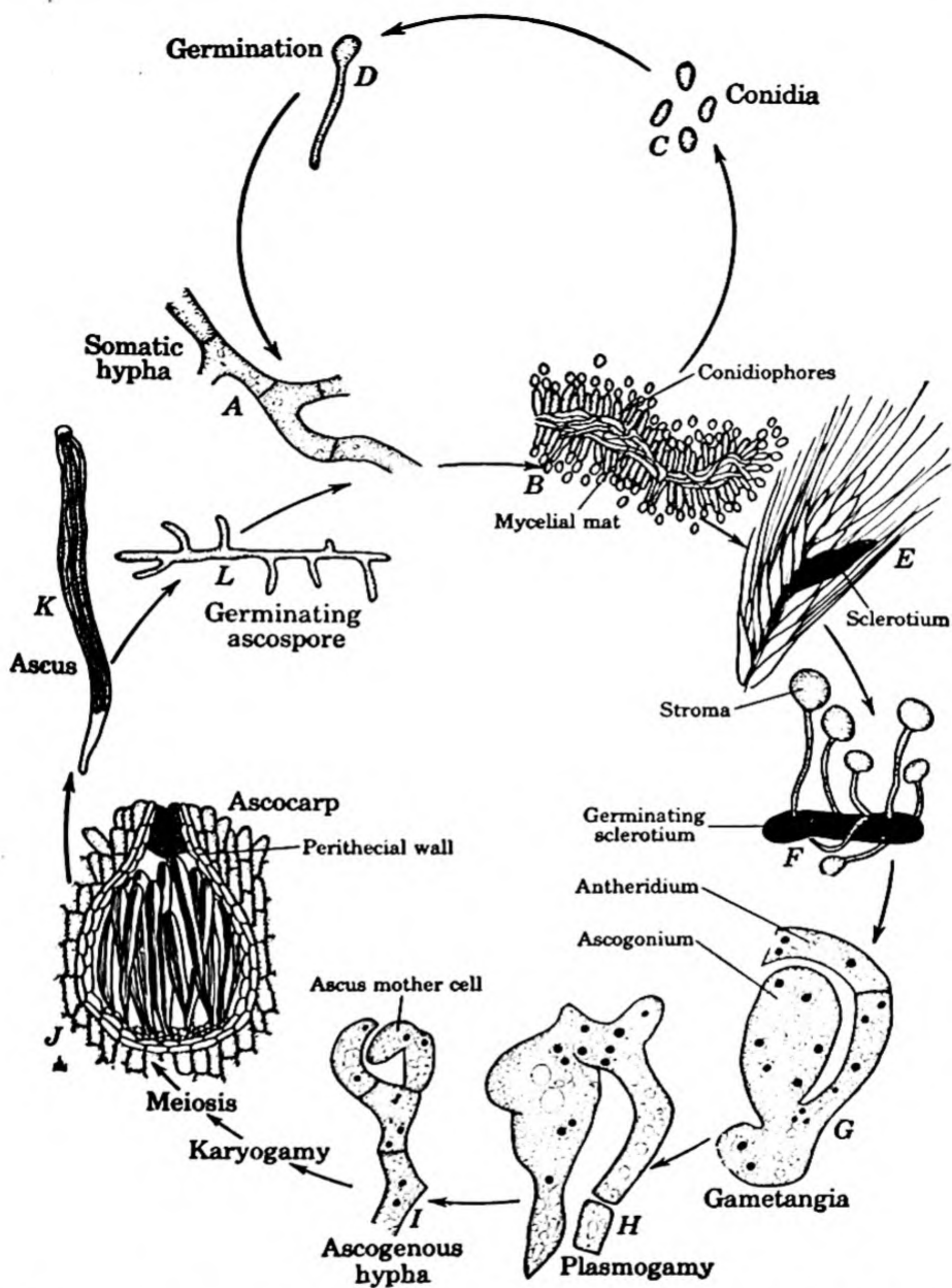


Figure 117. Life cycle of *Claviceps purpurea*. A, D, constructed; G–I redrawn from Brefeld, in Engler and Prantl, 1897, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^{oo}, Wilhelm Engelmann, Leipzig.

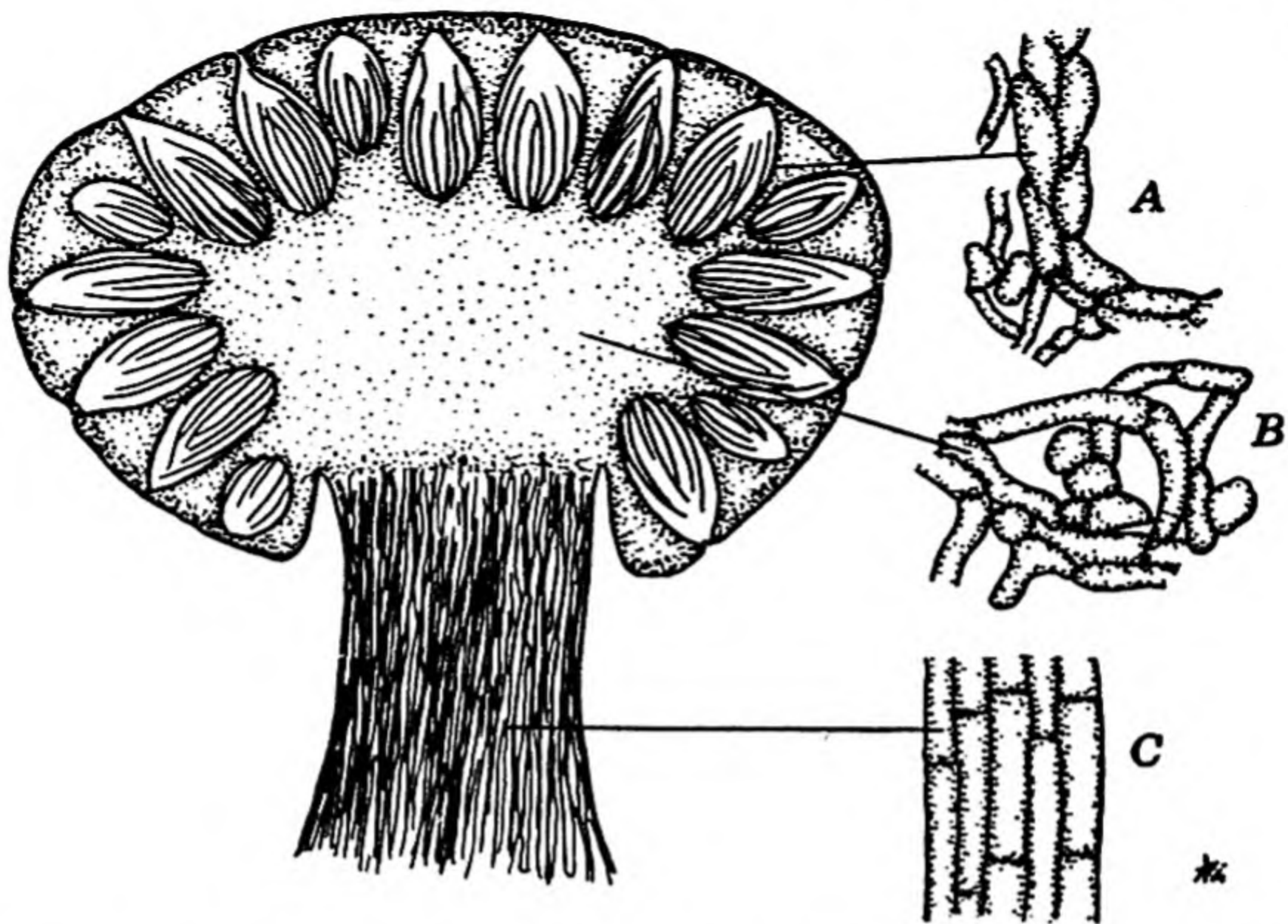


Figure 118. *Claviceps purpurea*. Stroma with embedded perithecia. A. Structure of perithecial wall. B. Structure of stromatal head. C. Structure of stalk.

where they pass the winter. The following spring, the sclerotia germinate and form several long-stalked, mushroom-like, dark purple stromata with globose heads. These stromata, which are about three-eighths of an inch tall, are easily visible (Figure 117F). Within these stromatal heads and just below their surface, arise a number of minute cavities surrounded by the pseudoparenchymatous stromatic tissue. Each of these cavities contains a single, multinucleate ascogonium at the base of which one or more multinucleate antheridia arise (Figure 117G). Plasmogamy now takes place between one of the antheridia and the ascogonium, the male nuclei migrating into the female organ (Figure 117H). The details of ascus formation have not been worked out, but we presume that they do not differ essentially from those of similar Ascomycetes. While the asci are forming, thin perithecial walls develop around the sexual apparatus within the stromatal heads, forming definite perithecia which open out on the surface of the stroma through a long, neck-like ostiole (Figures 117J and 118). Each mature perithecium bears several elongated, cylindrical asci, each containing eight thread-like ascospores (Figure 117K).

Whereas the mycelium of *Claviceps purpurea* parasitizing the rye plant is responsible for the plant disease known as ergot, the sclerotia of the fungus, which contain a number of poisonous alkaloids, are responsible for poisoning animals, including man, thus causing a condition known as ergotism. Cattle are often poisoned by grazing on grasses which carry the sclerotia of the fungus, or in fields in which the sclerotia are lying. In the past, because of improper methods used in cleaning flour, death of human beings from ergot poisoning was not uncommon in countries where the consumption of rye bread is high. With modern methods of milling, ergotism in human beings has been greatly reduced, but once in a while we read of a mass poisoning of people even today. In August 1951, for example, the American press¹ reported that a large number of people in the village of Pont-St. Esprit in France were suddenly attacked by what at first appeared to be a mysterious malady but which was soon diagnosed as ergotism. The symptoms were described in detail, and photographs of the suffering and the dead supplemented the gruesome reports.

Ergotism is much more common as a disease of domestic animals, however. Cattle which graze in infected fields are regularly poisoned by the sclerotia of this fungus.

The sclerotia of *Claviceps purpurea* are used in medicine for the preparation of a powerful abortifacient, which is also utilized in controlling hemorrhage during childbirth. So valuable is this drug that a number of studies have been conducted in an effort to discover a method for artificially infecting plants with *Claviceps purpurea* for the establishment of ergot farms. Pharmaceutical companies, however, are much more interested in a method for growing the fungus in liquid culture in vats, as they grow *Penicillium* for penicillin production. Although *Claviceps purpurea* grows easily in culture, no one has succeeded in inducing sclerotial formation outside the host plant.

orders CORONOPHORALES and CORYNELIALES

Too little is known about these orders to warrant discussion in an introductory book. The asci in both groups are said to be unitunicate, and the ascocarps to be ascostromata. If this is true, the correlation between unitunicate ascus and perithecium, and bitunicate ascus and ascostroma, appears to break down in these forms.

¹ *Life Magazine*, September 10, 1951; *New York Times*, August 29, 1951.

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15 series

DISCOMYCETES

cup fungi, morels, and truffles

Introduction. The Discomycetes include the cup fungi, the earth tongues, the morels, and the truffles. You can recognize most of them by their cup- or disc-shaped fruiting bodies which are produced on the ground, on buried sticks, rotten logs, overwintered leaves or fruits, or on animal dung. The fruiting bodies (apothecia) of some species are brilliantly colored: red, yellow, or orange. Those of others are brown, blending with the dead tree leaves among which they grow on the forest floor. A few are black. Besides the typical cups or discs, there are sponges, and bells, and saddles, and tongues, and brain-like fruiting bodies, and even some that resemble small leather bags filled with jelly. But all these different kinds of apothecia have one characteristic in common—they are open; they bear their asci on the surface or in large, open cavities, and they puff their spores out in clouds and in some cases with a hiss. The truffles, which also belong here, are the ever-present exception, and seemingly defy all the rules. Their fruiting bodies are underground, they are closed, and their spores remain imprisoned until some animal digs up the truffle for food and scatters the ascospores while devouring the ascocarp.

An apothecium (Figure 119) consists of three parts: the hymenium, the hypothecium, and the excipulum. The hymenium is the layer of asci which lines the surface or hollow part of the disc, cup, saddle, or other structure. It is made up of club-shaped or cylindrical asci, usually with many or few paraphyses among them. These may be as long as the asci, longer, or somewhat shorter. In some apothecia the tips of the paraphyses may be branched, and the tips of the branches may unite above the asci and form a layer called the **epithecium** (pl. *epithecia*; Gr. *epi* = upon + *theke* = a case). The **hypothecium** (pl. *hypothecia*; Gr. *hypo* = under + *theke* = a case)

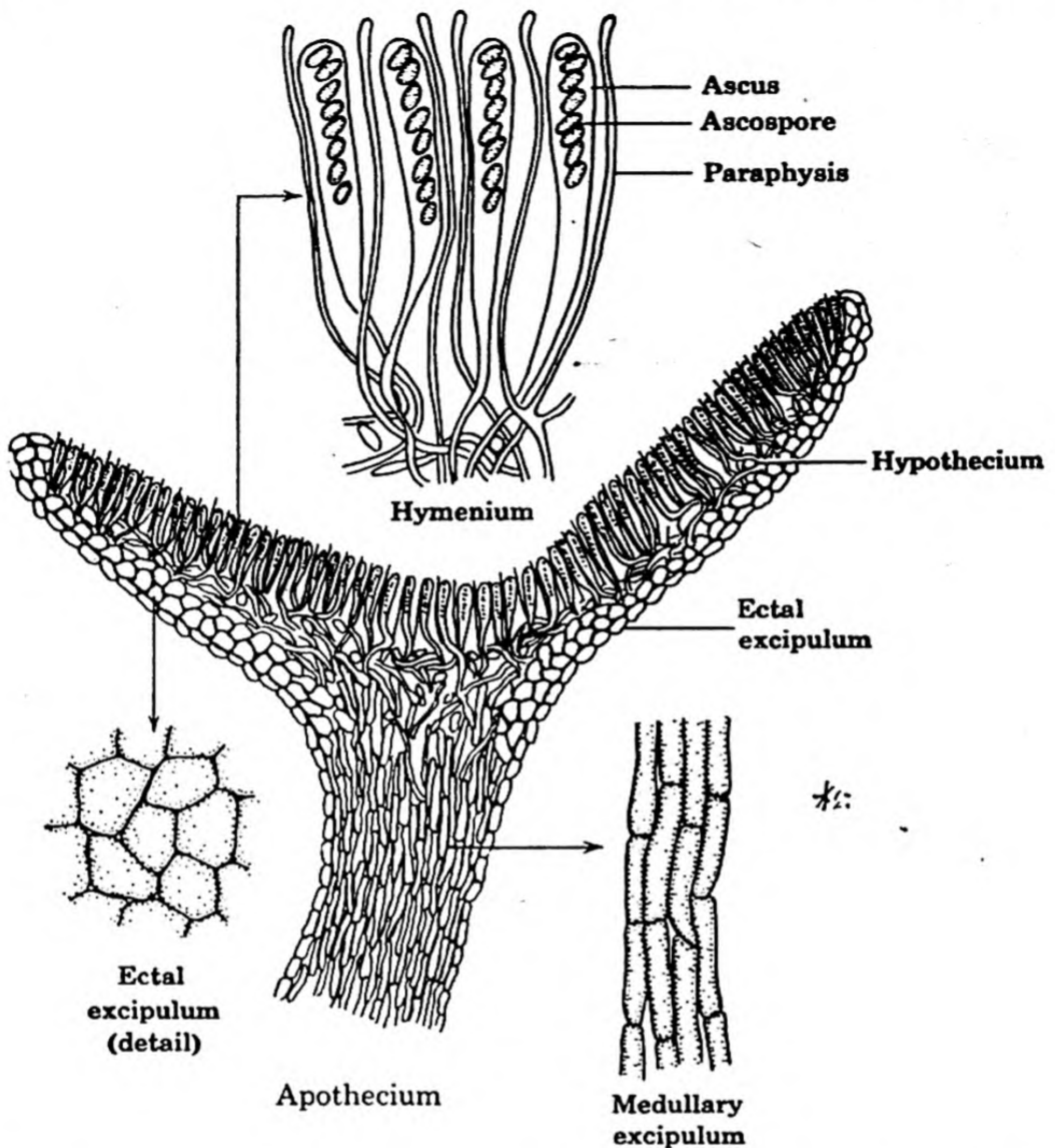


Figure 119. Diagram of a section through an apothecium. The main body may consist of several types of tissue.

is a thin layer of interwoven hyphae immediately below the hymenium. The apothecium proper (*i.e.*, the fleshy part of the ascocarp which supports the hypothecium and hymenium) is called the **excipulum** (pl. *excipula*; N.L. *excipulum* = receptacle). Using Korf's terminology, we regard the excipulum as consisting of two parts: the **ectal excipulum**, which is the outer layer of the apothecium, and the **medullary excipulum**, which is the inner portion.

Several types of tissue may be combined in an apothecium. Korf summarizes and illustrates the various types of tissues in his 1958 paper, "Japanese Discomycetes Notes I–VIII." A knowledge of the apothecial tissues is necessary for the accurate identification of discomycete fungi.

We classify the Discomycetes which form their ascocarps above ground (epigean) into two large groups based on their method of releasing spores from the asci. In the first group, the inoperculate Discomycetes, the asci release their spores through an apical, circular perforation. In the second group, the operculate Discomycetes, each ascus has at its tip a hinged cap or lid-like structure, the operculum, which opens and permits the escape of the ascospores. Less frequently, instead of an operculum, a longitudinal slit opens and releases the spores during discharge from the ascus (Figure 87D). In both these groups the ascospores are generally shot off violently.

The inoperculate Discomycetes consist of the orders Ostropales and Helotiales. The operculate Discomycetes include the Pezizales. The Tuberales are hypogean. You will find these four orders included in the key on page 267.

Many of the Discomycetes have been studied cytologically, and much information has been obtained from them. Because of their size, their fruiting bodies provide excellent material for study. Many of them, however, have not been grown successfully in culture, and few of those that have been grown have produced ascocarps.

The evolutionary position of the Discomycetes is in dispute. The phylogenists who support the view that the Ascomycetes originated from the red algae place the Discomycetes near the base of the evolutionary tree, and derive the Taphrinales from them by reduction. Those who subscribe to the zygomycetous origin of the Ascomycetes consider the Pezizales more advanced forms, possibly derived from pyrenomycetous or plectomycetous ancestors.

EPIGEAN INOPERCULATE DISCOMYCETES

order OSTROPALES

The Ostropales include those inoperculate Discomycetes in which the ascospores are thread-like and frequently septate, eventually breaking up into segments. The asci are elongated, and their walls are greatly thickened at the ascus apex, allowing only a very narrow canal through the center. Miller (1949) points out the similarity of

the ascus of the Ostropales to that of the Clavicipitaceae in the Pyrenomycetes. The Ostropales are of little economic importance and are not very frequently encountered.

order HELOTIALES

The Helotiales, the larger of the two orders of inoperculate Discomycetes, have either cup- or disc-shaped apothecia with asci only slightly thickened at the apex, and with ascospores which are round, elliptical, or elongated, but seldom thread-like.

Many of the Helotiales live saprobically on the soil, on dead wood, on dung, or on other organic matter from which they draw nourishment. Some of them are parasitic on plants, however, and are among our worst fungous enemies. Among the latter are *Monilinia fructicola*, the cause of brown rot of stone fruits; *Sclerotinia sclerotiorum*, the cause of lettuce drop and other vegetable diseases; and *Stromatinia gladioli*, the cause of gladiolus corm rot. Tar spot of maple (*Rhytisma acerinum*), leaf spot of alfalfa (*Pseudopeziza medicaginis*), black spot of quince and pear (*Diplocarpon soraueri*), and needle cast of conifers (various fungi), to mention only a few, are other plant diseases caused by members of the Helotiales which sometimes assume serious proportions.

Different workers have variously subdivided this very large order into a number of families. These families are not clearly delimited, however, and considerable confusion has resulted in the past. Only four of the seven or eight families in this order will be discussed below.

family PHACIDIACEAE

This family, which some consider as representing a transitional stage between the perithecial and apothecial Ascomycetes, now includes some genera which were formerly placed in the Hysteriales. The ascocarps, which most mycologists regard as apothecia, are produced within the substratum consisting of plant tissue, and are covered by a black stroma. *Rhytisma acerinum*, the cause of tar spot of maples, and the needle cast fungi, belonging to the genera *Lophodermium*, *Hypoderma*, *Hypodermella*, etc., are examples of fungi now included in this family. In the more traditional classification systems which you will find in the older keys, *Rhytisma* was placed in the order Phacidiales (not recognized here), while *Lophodermium* and other related genera were included in the family

Hypodermataceae of the Hysteriales. Nannfeldt (1932) removed the Hypodermataceae from the Hysteriales and, together with *Rhytisma* and related genera, incorporated them into the Phacidaceae, which he placed in the Helotiales.

Korf (1958), Dennis (1960), and Martin (1961) continue to recognize the Phacidiales as a distinct order, Korf expressing the opinion that they are more closely related to the Sphaeriales than to the other Discomycetes.

Rhytisma acerinum (Pers.) Fr.

The ascocarps of *Rhytisma acerinum* overwinter in the fallen, dead maple leaves. The flat, circular, black, tar-like stromata, which bear the apothecia within them, give the disease its name. The surface of each mature stroma is characterized by radiate fissures along which the stroma splits above the apothecia in the spring (Figure 120L). The apothecia are small, saucer-shaped structures. When the stroma splits open, long needle-shaped ascospores are released in great numbers from the apothecia by a puffing action which liberates visible clouds of spores, whereupon air currents pick them up and distribute them.

Reaching a susceptible host, the ascospores germinate by germ tubes (Figure 120M) which invade the maple leaf through the stomata and infect the epidermal and mesophyll cells (Figure 120A). The mycelium grows within the epidermal cells and eventually forms the stroma. This causes the infected epidermal cells to split horizontally and form a pocket in which the fungus develops its reproductive structures. Meanwhile the fungal hyphae secrete a black, gummy substance which cements together hyphal and host elements in the center of the infected spot. The top of this black stroma, which contains the upper half of the split epidermal cells, bulges over the leaf and looks like a spot of tar.

Structures which resemble acervuli now form within the stroma. These appear as small pimples with a minute hole in the center (Figure 120B). These structures, the spermogonia, produce enormous numbers of minute, rod-shaped "spermatia" (Figures 120C-E) which exude through the perforations in the stroma above them. We have not discovered the function of the spermatia; no investigator has been able to germinate them or to produce infection on maple leaves by spraying with spermatial suspensions. Although in the literature they are called conidia, it is possible that they are true spermatia, and the fact that no antheridia have been discovered

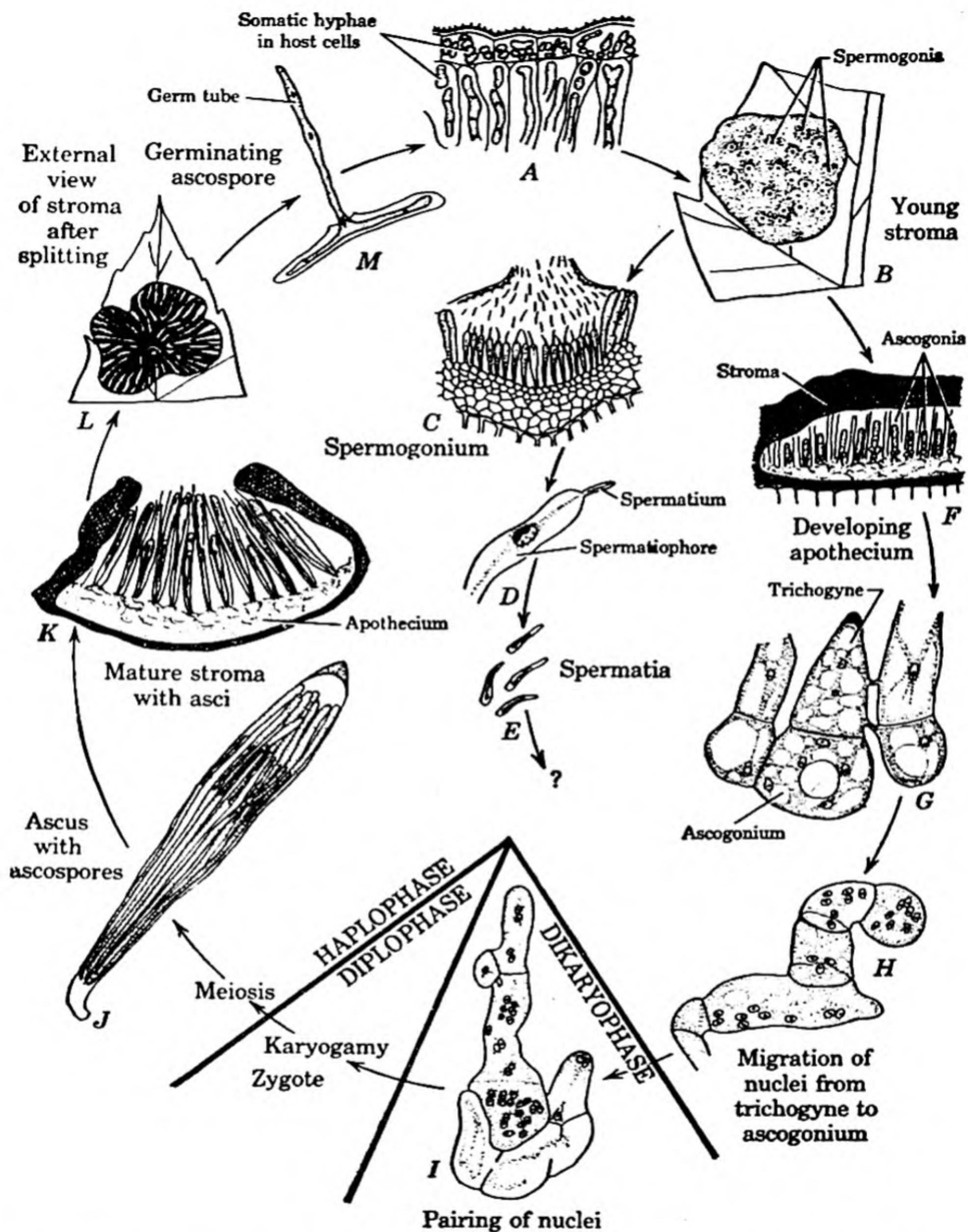


Figure 120. Life history of *Rhytisma acerinum*. A, C-I, M, redrawn from Jones, 1925, *Ann. Bot.*, 39:41-75.

in this fungus tends to support this theory. As I shall explain in a later paragraph, however, Jones' studies (1925) indicated that no male organs are necessary for sexual reproduction.

No asexual method of reproduction has been found in *Rhytisma acerinum*, and it is not known how the fungus spreads during the growing season.

As the somatic hyphae continue to grow and spread, the stroma enlarges considerably beyond the spermogonial area and develops radiate wrinkles under which the apothecia form. Toward the end of the season ascogonia are produced (Figure 120F) in the apothecial initials, which form profusely within the stroma around the spermogonia and, in some cases, within them.

According to Jones (1925), each multinucleate ascogonium bears a multinucleate trichogyne (Figure 120G). The septum which separates these two parts partially dissolves, and the trichogynal nuclei pass into the basal ascogonial cell (Figure 120H) and pair with the ascogonial nuclei. The nuclear pairs then pass into the ascogenous hyphae, which grow out of the ascogonium, and the asci and ascospores are formed by the usual hook method (Figure 120I).

The fungus passes the winter in the fallen leaves in the immature ascocarp stage, developing slowly during the winter months. In early spring, the asci (Figures 120J, K) complete their development, and, when the stroma splits along the preformed, radiate lines, the needle-like ascospores are forcibly ejected.

family SCLEROTINIACEAE

The Sclerotiniaceae comprise one of the largest families of all inoperculate Discomycetes and, from the economic standpoint, the most important one. Most fungi classified here live parasitically on plants, but can be easily cultured. Apothecial initials arise from stromata or sclerotia. The apothecia are of medium size, generally brown, and are most often borne on long stalks, although some species produce apothecia that are short-stalked. The ascospores are generally hyaline, one-celled, oval or somewhat elongated. In *Monilinia oxycocci* four of the ascospores in each ascus are much smaller than the other four. The arrangement of the spores indicates that ascospore size is probably controlled by a pair of alleles (Buchwald, 1956).

The characters of the sclerotia, of the stromata, and of the conidial stages differentiate the various genera of the Sclerotiniaceae.

Whetzel (1945) subdivides the family into fourteen genera, many of which include a number of important plant pathogens.

Monilinia fructicola (Wint.) Honey

Monilinia fructicola, the cause of brown rot of peach and other stone fruits, will be discussed as an example of the Sclerotiniaceae. It or related species (*Monilinia fructigena*, *Monilinia laxa*) occur in all regions of the world where stone fruits or pome fruits are grown, causing considerable damage annually.

The mycelium of *Monilinia fructicola*, which begins as a germ tube emerging from the ascospore or conidium (Figures 121A, D, N) in the spring, invades either the blossoms of a susceptible host, causing blossom blight, or the young twigs or leaves, causing twig blight or leaf blight, respectively. Soon after the mycelium reaches a certain stage in its growth, it produces long, branched conidiophores (Figure 121B) which rapidly break up into chains of oval or lemon-shaped conidia (Figure 121C). This is the *Monilia* stage of the fungus, so called because it belongs to the form-genus *Monilia* of the Deuteromycetes (see page 410). The conidia break off easily from the chain and are scattered by the wind. If they reach a susceptible host, they germinate in the presence of water; each conidium produces a germ tube, invades the host, and thus spreads the disease. In wet years brown rot epiphytotics occur, and this disease is without doubt the worst enemy of the peach grower. New conidia mature every few days, repeating the asexual cycle of the fungus, so that in a single growing season several generations of conidia form.

Young peach fruits are resistant to the invasion of the fungus, but as they approach maturity their resistance decreases and the fungus invades through hair sockets, insect punctures, or other wounds and causes the familiar brown rot. The infected fruit first shows a soft brown spot. The mycelium of the fungus spreads rapidly, secreting ahead a powerful enzyme which dissolves the middle lamellae of the host cells and renders tissues soft. Invasion of the softened tissues by the mycelium follows immediately, and eventually the hyphae penetrate the entire fruit, which shrivels and mummifies (Figure 121E). Ripe fruit may either fall from the tree and mummify on the ground, or mummify on the tree and remain clinging to the branches all winter long. The mummies are a mass of dried fruit tissue, completely penetrated by the mycelium of the fungus and covered with conidia. The mycelium thus overwinters in the mum-

mified fruit, and also in the small twig cankers which have been formed by the early infection of the young twigs. It is possible also that some conidia may remain alive and initiate new infections in the spring. Mummies which are left clinging on the branches constitute an excellent source of infection in the spring, the mycelium within

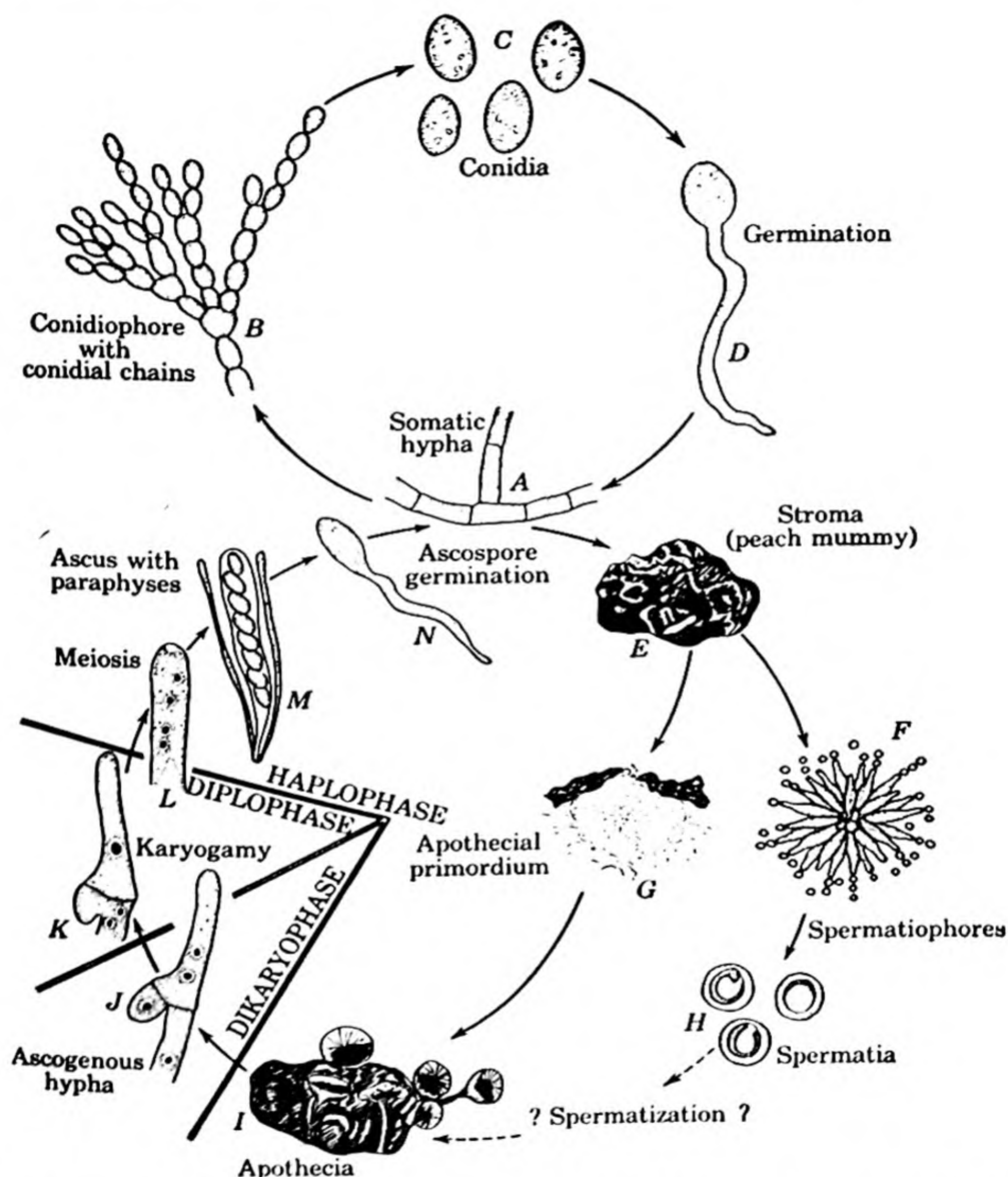


Figure 121. Life cycle of *Monilia fructicola*. C, H, J-L, redrawn from Heuberger, 1934, Maryland Agr. Exp. Sta. Bull., 371:167-190.

them producing its first crop of conidia with the first signs of warm weather.

The fruit which has mummified on the ground becomes partially buried in the soil and after one to three years produces the apothecia of the fungus. The mycelium in the mummy is a type of stroma from which the apothecial initials originate. The events which lead to the development of the apothecia in *Monilinia fructicola* have not been discovered. However, it is highly probable that the details of the life history of *Stromatinia* (*Sclerotinia*) *gladioli*, which Dr. Drayton of the Dominion Laboratories in Ottawa, Canada, discovered, also hold true for *Monilinia fructicola*. Drayton (1934) found that *Stromatinia gladioli* produces small, globose spermatia borne on spermatophores. Its mycelium also forms a stroma from which columnar receptive (female) structures arise. These structures contain the coiled ascogonia of the fungus. When compatible spermatia are transferred to the receptive columns, spermatization causes the columnar structures to elongate and develop into fertile apothecia, which bear asci and ascospores. Apothecia form only if spermatization takes place. Dr. Drayton's paper on the sexual mechanism of *Stromatinia gladioli* is one of the milestones of mycology.

Monilinia fructicola commonly produces spermatia (Figures 121F, H), or microconidia as we also call them, the function of which no one has yet discovered. Apothecial fundaments are formed in large numbers on peach mummies on the ground (Figure 121G). These probably correspond to the columnar, receptive structures of *Stromatinia gladioli*. Although no observer has established spermatization in *Monilinia fructicola*, the fact that only some of the apothecial fundaments develop into mature apothecia (Heuberger, 1934), while most of them remain undeveloped, may indicate that only those that are spermatized ever form asci.

Regardless of their developmental history, the long-stalked apothecia (Figure 121I) are produced in great numbers in the spring on peach mummies which have passed the winter on the ground, and develop asci and ascospores in the usual manner (Figures 121J-M). By a puffing action, the asci forcibly expel their ascospores, which are released in clouds. Air currents carry the spores to the blossoms, twigs, and young leaves of the trees above, and, if weather conditions are favorable, the ascospores initiate infection and start a new life cycle.

The production of apothecia on the grounded mummies and their absence from the aerial mummies which cling to the tree branches have not been explained satisfactorily. It may be that conditions on

the ground level, which favor spermatization and development of the archicarps, are absent at the level of the tree branches. Whether it is a question of a continuous film of water which carries the right spermatia to the right receptive organs, or whether some other factor operates, remains for someone to discover.

family GEOGLOSSACEAE

This is a family of interesting saprobic Ascomycetes the ascocarps of which are modified into tongue-, club-, or fan-shaped apothecia with long stalks (Figure 122). You may find them in the woods, growing on the soil, on decaying leaves or wood, or on other organic matter which contains considerable moisture.

The hymenium of the Geoglossaceae covers the surface of the upper portion of the mature ascocarp. The asci are elongated, and the ascospores vary from one- to many-celled, and from hyaline to dark brown.

The family is usually divided into two tribes: the Geoglosseae, with ascocarps which are club-shaped, spoon-shaped, or capitate (L. *caput* = head), and the Cudonieae, with pileate (L. *pileus* = cap) ascocarps. *Geoglossum* with black or brown club-shaped apothecia and *Spathularia* with spoon-shaped ascocarps are probably the most commonly encountered genera of the first tribe. The genus *Leotia* with gelatinous ascocarps, which has been included in the Cudonieae by many authors—often reluctantly—was transferred to the Helotiaceae by Imai and Korf (Korf, 1958).

family CYTTARIACEAE

The Cyttariaceae are confined geographically to the southern hemisphere, where they are parasitic on various species of *Nothofagus*, the southern beech.

As Discomycetes go, the Cyttariaceae are a peculiar group, their ascocarps being embedded in fleshy, globose stromata produced in large clusters. The position of this family is uncertain, but the structure of their asci places them in the inoperculate Discomycetes (White, 1954) and, according to Chadeaud (1960), in the Helotiales.

As a result of infection, a gall is formed on the branches of the host. The mycelium is present in the parenchyma of the gall. From a mass of hyphae just below the surface of the gall, a pear-shaped stroma eventually develops in which the apothecial initials are

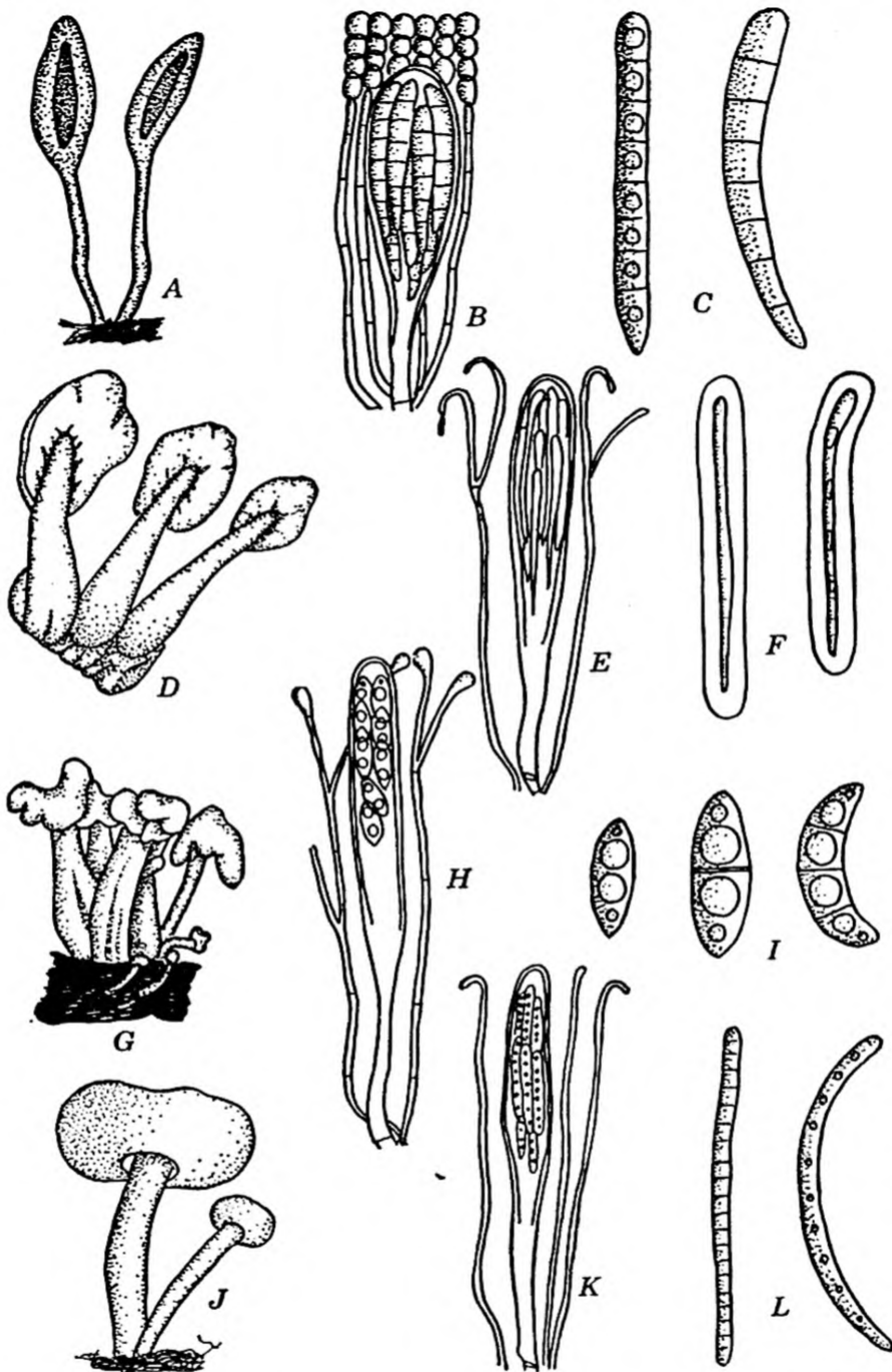


Figure 122. Geoglossaceae. A-C. *Geoglossum ophioglossoides*. D-F. *Spathularia clavata*. G-I. *Leotia gelatinosa*. J-L. *Cudonia circinans*. *Leotia* has been transferred to the Helotiaceae by Imai and Korf (1958). Redrawn from Winter, 1896, in Rabenhorst's *Kryptogamen Flora*, Vol. III, E. Kummer, Leipzig.

formed. These grow while the stroma enlarges, and produce hymenia consisting of asci and paraphyses. The asci arise from croziers, probably in the usual manner (White, 1954). Cytological details are lacking.

EPIGEAN OPERCULATE DISCOMYCETES

order PEZIZALES

The Pezizales are a large order of operculate Discomycetes. Their apothecia may be open from the very beginning or may be closed at first, opening later and releasing the ascospores. The Pezizales include a wide variety of fungi. Some have large fruiting bodies 4 or 5 inches in diameter; others have minute ascocarps less than a millimeter across; some stand out as colorful, beautiful specimens, whereas others are brown or black; some are edible, a few are poisonous. Most Pezizales are saprobic, living on dead wood, soil, or humus; and, except for the edible and poisonous species, they are of little direct importance to us. We know the majority of Pezizales only by their ascogenous stages; the imperfect (conidial) stages of most have not been found if, indeed, they exist.

The Pezizales form the large, conspicuous, often brilliantly colored cups which we find in the woods from early spring to late fall; they also form some of the smallest of apothecia, which go unnoticed by anyone who is not particularly searching for them. Many species such as *Peziza badio-confusa*, whose large brown apothecia grow on the ground in deciduous woods, are sometimes difficult to see because the apothecia may be partially covered with leaves. If you remove the leaves and wait for a few minutes or, better still, blow gently over the cups, you will be able to observe the puffing of the apothecia and the release of the ascospores in clouds. Dr. A. H. R. Buller, the prominent Canadian mycologist who contributed enormously to the understanding of the mechanics of spore discharge, stated (Buller, 1934) that, if you take an apothecium of any one of a large number of species he tested and place it against your ear, you can hear a hissing sound at the time of ascospore release, and even feel the impact of the spores as they are discharged against the folds of the outer ear in a jet of liquid.

Classification. The classification of the Pezizales has not been stabilized as yet. We shall discuss the order under three families: Sarcoscyphaceae, Pezizaceae, and Helvellaceae. These may be separated as follows:

SIMPLIFIED KEY TO THE FAMILIES OF THE ORDER PEZIZALES

- | | | |
|-----|--|------------------------|
| A. | Asci sub-operculate ¹ | <i>Sarcoscyphaceae</i> |
| AA. | Asci operculate | |
| | B. Apothecia not differentiated into stipe and pileus | <i>Pezizaceae</i> |
| | BB. Apothecia clearly differentiated into stipe and pileus | <i>Helvellaceae</i> |

¹ See following section and glossary for definition.

For other views on the classification of the Pezizales see Seaver (1928), LeGal (1947, 1953), Nannfeldt (1937, 1949), Korf (1954), Dennis (1960), and Martin (1961).

family SARCOSCYPHACEAE

This family was erected by Mme. LeGal in 1947, but a complete description was first given by Nannfeldt in 1949. The most important character which separates this family from the others is the structure of the ascus. Chadeaud (1946) described this ascus as para-operculate. Most other authors use the term sub-operculate. The ascus possesses a thickened apical ring capped by a plug or hinged operculum, its opening often oriented obliquely. The asci are long and slender, with a flexible base. The ascospores are colorless, variously ornamented but never septate.

The Sarcoscyphaceae form generally large stipitate, often brilliantly colored apothecia. The family is mainly tropical, but some species are cosmopolitan. Mme. LeGal (1947) subdivides the family into two tribes: *Urnuleae* and *Sarcoscyphaceae*. Of the *Urnuleae*, *Urnula craterium* is commonly encountered in our northern woods. You can recognize it easily by its dark brown or black, deeply cup-shaped clustered apothecia. This fungus is suspected of being the perfect stage of *Strumella coryneoidea*, the cause of *Strumella* canker of oak and other forest trees (Davidson, 1950; Fergus, 1951). *Galiella* and *Sarcosoma* are among the other genera in this tribe. *Sarcosoma* is interesting because of its heavy gelatinous fruiting bodies. The large brown apothecia of *Sarcosoma globosum* (Figure 123) sometimes measure as much as 3 or more inches in height and over 2 in diameter. The upper portion of the apothecium is hollowed out and bears the hymenium. The basal portion is filled with a jelly which causes the skin-like ectal excipulum to bulge.



Figure 123. *Sarcosoma globosum*. From Kodachrome transparency by the author.



Figure 124. *Sarcoscypha coccinea*. From Ansco color transparency by the author.

Probably the majority of the Sarcoscyphaceae are tropical fungi. *Cookeina* and *Phillipsia* with red or yellow apothecia adorn tropical forests around the globe. In the temperate zone, one of the earliest and most beautiful species is the scarlet cup fungus (*Sarcoscypha coccinea*), which you can find from March to May, depending on the season and the locality, producing its red apothecia in clusters on buried sticks (Figure 124). The spores germinate by one of two methods. Some spores produce the usual germ tube which develops into a mycelium. Other spores upon germination produce a short germ tube which cuts off tiny conidium-like structures (Alexopoulos and Butler, 1950; Rosinski, 1953). Spores from the same ascus have been observed in our laboratory to vary in their method of germination. What causes this difference is an interesting problem which should be studied. Unfortunately, no one has been able to induce ascocarp formation in culture, and the inheritance of such characters cannot be investigated by direct methods.

The largest of the Sarcoscyphaceae is *Wynnea americana*, a rare discomycete known only from a few localities in the United States. The spoon-shaped apothecia, which reach a height of 13 cm., are dark brown to black and arise in clusters from large sclerotia (Figure 125).

family PEZIZACEAE

The apothecia of the Pezizaceae are mostly cup-, disc-, or lentil-shaped. They may be sessile to stalked, minute to very large, brightly colored to dark brown, smooth, velvety, hairy, or bristly. Recognizing this great variability, most authors have divided the Pezizaceae into several tribes. One proposal (Korf, 1954) recognizes eleven tribes, two of which, however, comprise the traditional family Helvellaceae of other authors.

Whereas the Sarcoscyphaceae are invariably *epixylous* (Gr. *epi* = upon + *xylon* = wood), many of the Pezizaceae grow on the ground or on the dung of animals. Wood-inhabiting species, however, are plentiful as well.

Among the more common species which you can find in any woods throughout the season and should learn to recognize at sight is *Scutellinia scutellata*, whose blood-red apothecia, 2–12 mm. in diameter, grow on a variety of substrata, but most often on rotten wood or on bark among mosses. The apothecia are covered externally with dark brown hairs. *Peziza vesiculosa* is one of the larger cup fungi.



Figure 125. *Wynnea americana*. Courtesy Korf, 1949, *Mycologia*, 41:649-651.

The cups are crowded together on manure piles, well-fertilized gardens, greenhouses, etc. They are whitish or pale brown and exhibit minute pustules on the surface. The species is probably cosmopolitan.

Two species which occur on recently burned-over substrata are *Anthracobia melaloma* and *Pyronema omphalodes*. The former occurs on burned wood, the latter on burned ground and on sterilized or steamed soil. Both grow and fruit well in culture and have been used for cytological and developmental studies (Olive, 1950; Ro-

sinski, 1956; Wilson, 1952). *Anthracobia melaloma* is heterothallic. *Pyronema omphalodes* has been the object of study by several investigators over a long period of years and is the example most commonly used to illustrate the details of ascus development in the Ascomycetes (Figure 82).

Many of the Pezizaceae are coprophilous. Many species of the genera *Ascodesmis*, *Ascobolus*, and *Saccobolus* particularly, grow almost exclusively on dung, and some of them may even be specialized as to the animal on whose excreta they grow. *Ascodesmis porcina*, for example, grows mostly on the excreta of hogs. *Ascodesmis macrospora* is known only from the dung of mountain lion and jaguar. The apothecia of the three genera just mentioned are minute, ranging in size from 0.5 to 5 mm., except those of *Ascobolus magnificus*, on horse dung, which may reach an inch or more in diameter. The ascospores in these three genera are purplish, eventually turning to a dark brown, almost black. They are difficult to germinate and require special treatment such as heating. Dodge (1920) found that *Ascobolus magnificus* consists of two self-sterile strains which must be mated before apothecia are produced. The same situation is known to occur in several other species of *Ascobolus* and related genera. A study on sexual reproduction in *Ascobolus* is reported by Bistis in his excellent papers in the *American Journal of Botany* (1956b, 1957). He presents evidence of a hormonal mechanism which initiates plasmogamy by guiding the trichogyne of *Ascobolus stercorarius* to the oidia, which behave as spermatia. *Ascobolus* and related genera are often placed in the family Ascobolaceae (Dennis, 1960).

Most of the Pezizaceae seem to lack any conidial stage. However, conidia have been discovered in *Peziza repanda*, *Peziza vesiculosa*, and *Patella abundans* among others. Microconidia are known in several species.

family HELVELLACEAE

The Helvellaceae include the morels (sponge mushrooms), the bell morels, the false morels, and the saddle fungi. Few of their life histories have been investigated, and relatively little is known about their biology. These fungi, however, warrant some discussion here because of their interest as table delicacies. Students who have been exposed to a course in mycology, however brief, should, I feel, learn to enjoy some of the physical as well as the intellectual pleasures of the science.

All the Helvellaceae produce fairly large apothecia. You can recognize them readily and easily distinguish them from one another, once you become acquainted with their general appearance and characteristics.

genus *MORCHELLA*

The true morels belong to the genus *Morchella*, which contains several species. The conic morel (*Morchella conica*), the hybrid morel (*Morchella hybrida*), the delicious morel (*Morchella deliciosa*), the common morel (*Morchella esculenta*) (Figure 126), and the thick-stemmed morel (*Morchella crassipes*) are some of the species we recognize as distinct. All have apothecia with a thick stalk and a pitted or sometimes ridged pileus which looks like a sponge. The color varies from a dirty grayish white to a dark brown, depending on the species and the age of the specimen. The size varies from 1 inch or less to 4 or 5 inches in height. *Morchella crassipes* has the largest apothecia of all the species mentioned, and perhaps the most delicious flavor.



Figure 126. *Morchella esculenta*. From Kodachrome transparency by the author.

The hymenial layer of a morel lines the pits of the pileus. It consists of long, cylindrical, operculate asci, each containing eight ascospores, and of elongated paraphyses interspersed among the asci. The ascospores are large, colorless, oval, and, at maturity, eight-nucleated.¹

All true morels are edible and delicious. Indeed, with the possible exception of the European truffles, they are the most delectable of all the fungi. Although, as I said before, the various species of *Morchella* differ greatly in size, color, and markings, once you learn to recognize the general aspects of the genus, you will not confuse any other fungi with the morels.

The morels themselves are, of course, the ascocarps of the fungus, the mycelium of which grows in the ground, nourishing itself on organic material. Although saprobic, morels have not been grown in pure culture to the fruiting stage. Mycelial colonies can be obtained with relative ease, but no one has been able to obtain ascocarps in culture. There are various reports of people who have "planted" morels by crumpling fresh or dried ascocarps on the ground, and have harvested a crop the next season. It has been reported that in France (Heim, 1936) a rich crop was harvested as the result of crumpling dried morel ascocarps on ground previously "fertilized" with apple mash obtained from cider factories. A small fortune awaits the person who develops a successful method for growing morels commercially.

Physiological studies report that a pH relatively higher than the optimum for most fungi is best for the growth of *Morchella esculenta*; that starch, maltose, fructose, turanose, glucose, and sucrose all are good sources of carbon; and that both ammonium and nitrates can be utilized in addition to urea, some amino acids, and—surprisingly enough— NaNO_2 as N sources (Brock, 1951). Wood extract added to a synthetic medium increased mycelial growth of *Morchella esculenta* and *Morchella crassipes*. A growth factor other than the B vitamins was held responsible for the beneficial effect (Robbins and Hervey, 1959).

genus *VERPA*

The genus *Verpa* includes the bell morels. These fungi produce large apothecia with long, thick, white, somewhat flattened stalks bearing brown, bell-shaped caps which, because of their relatively

¹ Communication by L. R. Batra to the Mycological Society of America, August 29, 1961.

small size, appear disproportionate to the stalks. The cap of the ascocarp is attached to the stalk in the center and the margin is free. The outer surface of the cap is either smooth or longitudinally ridged. The hymenium covers the outer surface of the cap. In the species *Verpa bispora*, the ascus contains but two ascospores. Like the true morels, bell morels are edible and of good flavor. However, it appears that consumption of large quantities of certain species of *Verpa* temporarily affects muscular coördination of some individuals.

genus *HELVELLA*

The genus *Helvella* contains the saddle fungi and the so-called false morels. As their name indicates, the saddle fungi have an irregular cap shaped like a saddle. This is generally borne on a heavily ridged stalk. *Helvella crispa* is one of the most common species of the saddle fungi.

The false morels, sometimes separated into several genera (*Gyromitra*, *Maublancomyces*, etc.), somewhat resemble the true morels. Their brown pileus, which may be quite large, is borne on a stalk that may be short or long, twisted or heavily ridged, and thick. In contrast to the true morels, the cap of the false morels is saddle-shaped, or convoluted and brain-like, rather than ridged or pitted and sponge-like as in *Morchella*.

There are several species, some of them cosmopolitan. *Helvella gigas*, *Helvella esculenta*, and *Helvella underwoodii* you will find in the spring. The first, as the name indicates, is the largest, its ascocarps often exceeding 6 inches in height and 4 inches in diameter. *Helvella underwoodii*, which is more or less saddle-shaped, is also quite large. *Helvella esculenta* has a wrinkled, dark, reddish brown head. *Helvella infula* produces its saddle-shaped apothecia in the summer and fall (Figure 127).

Some people eat false morels and find them delicious; others eat them and die! The most recent case of mass poisoning by *Helvella esculenta* (the name, by the way, means "edible!") was reported from Normandie, France, where at least seventeen persons who consumed cooked sporophores of this species became violently ill (Denis, 1961). The poison responsible is helvellic acid. Because people differ in their susceptibility to these fungi, you should learn to recognize the false morels and leave them alone.

All three of these genera (*Morchella*, *Verpa*, and *Helvella*) are spring mushrooms, the bell morels possibly appearing somewhat earlier than the others, but some species of *Helvella* are also found



Figure 127. *Helvella* (*Gyromitra*) *infula*. Courtesy L. R. Batra.

in the summer and fall. They are generally found in the woods growing in the soil among old leaves, but some species frequently grow on cultivated soil in orchards or in open fields of grass. Some morels are associated with certain conifers, and it is possible that they form mycorrhizae with them. The morel season is comparatively short, lasting about a month. In central Michigan, for example, morels generally appear early in May; by the first week in June they are gone—but not forgotten.

HYPOGEAN DISCOMYCETES

order TUBERALES

The Tuberales are the truffles, some of which epicureans prize highly as food in continental Europe. The ascocarps (genus *Tuber*, Figure 128A) are hypogean and remain closed in most species, liberating the ascospores only when the ascocarp decays or is broken by animals. The asci, in contrast to those of other Discomycetes, may be globose or widely oval, and the ascospores are often spherical (Figure 128D).

The truffles of commerce are native to France and Italy. With the

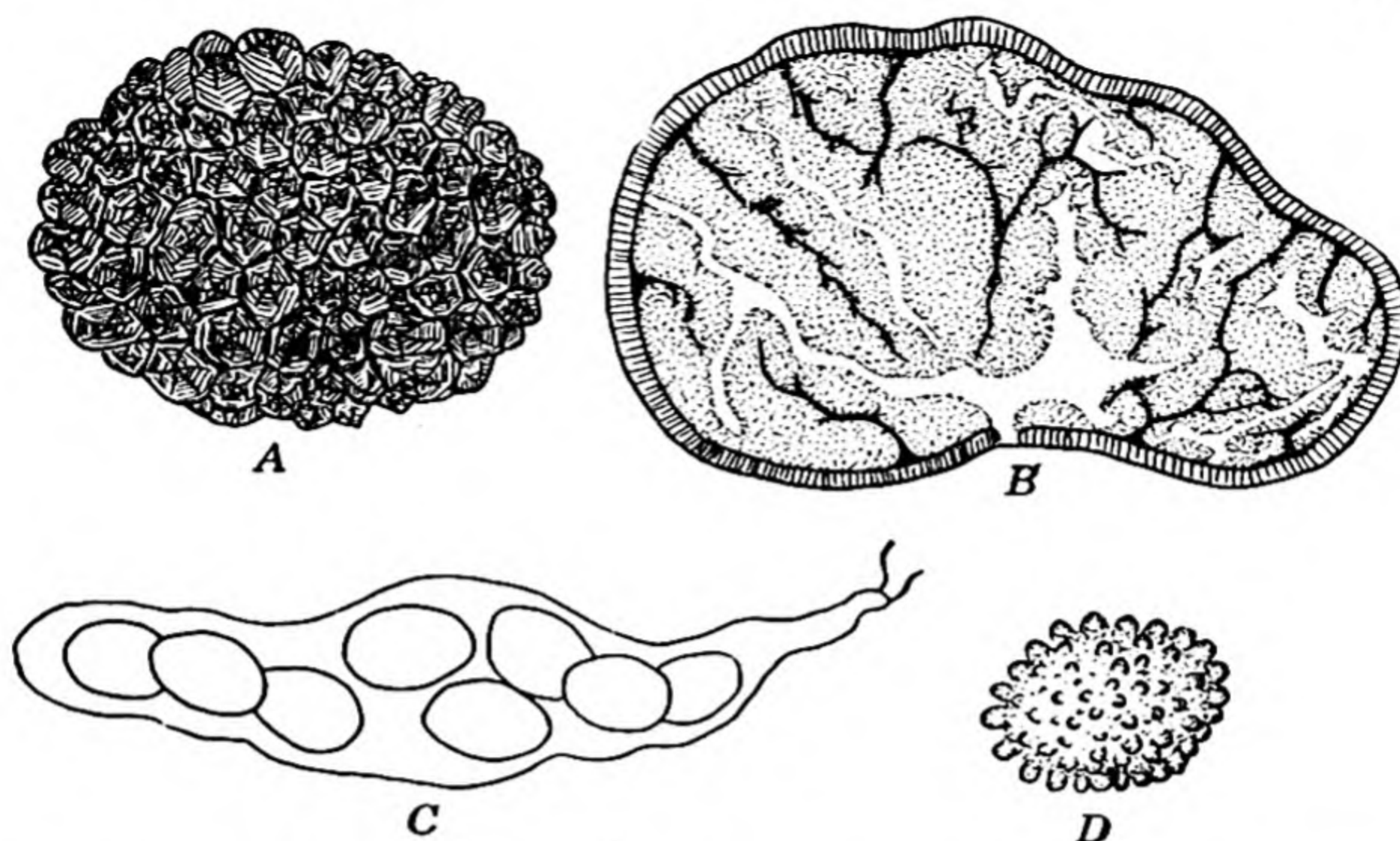


Figure 128. Tuberales. A. Ascocarp of *Tuber aestivum*. B. Section through ascocarp of *Tuber rufum*. C. Ascus of *Genea harknessii*. D. Ascospore of same. A, B, redrawn from Tulasne, in Engler and Prantl, 1897, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^{oo}, Wilhelm Engelmann, Leipzig; C, D, redrawn from Miss Gilkey, 1916, *A revision of the Tuberales of California*, Univ. Calif. Publ. Bot., 6:275-356, by permission of University of California Press, Berkeley.

help of trained dogs and pigs, which detect the odor of the truffles and dig them up, people gather them and offer them for sale in the markets. The order is represented by several species in the United States, known mostly from the Pacific coast states. Most of these produce small ascocarps which are not suitable as food. Miss Helen Gilkey of Oregon State College has written two monographs (1939, 1954) on the American Tuberales. For an entertaining as well as accurate account of the biology of the truffles read the section, "Fungus Partnerships with Other Plants," in Dr. Clyde Christensen's (1951) *The Molds and Man*.

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16 series
LABOULBENIOMYCETES
order
LABOULBENIALES

This is a rather large group of highly specialized parasites of insects and arachnids which occur mostly superficially on their hosts, seldom penetrating beyond the exoskeleton and causing no apparent injury.

The soma consists of a receptacle and its appendages. Male and female reproductive structures may be borne on the same individual or, in dioecious species, on different individuals. The receptacle is anchored to the host cuticle by a dark basal cell called the foot. In some species a rhizoid (haustorium) grows out of the basal cell and penetrates more deeply into the host.

The fungus obtains all its nourishment from the host, causing a dermatitis but without evidence of pathogenicity (Richards and Smith, 1956). Of considerable interest is Richards' report (1954) of the similarity in chemical composition of the parasitized host cuticle and the walls of the parasite.

Over 1500 species are known, all of them included in the single order Laboulbeniales.

The Laboulbeniales, although seldom collected, do not seem to be rare. If you examine the ants in an ant hill, for example, you are likely to find the species which attack these particular insects. I say "these particular insects" because the Laboulbeniales exhibit great host specialization, which has been verified by repeated observations and, more recently, by experimental cross-inoculations. Richards and Smith (1954) attempted to cross-inoculate five species of *Herpomyces* on fifteen species of cockroaches and found that they were very highly, but not completely, host specific. These workers also found that the species of *Herpomyces* used were stable in their

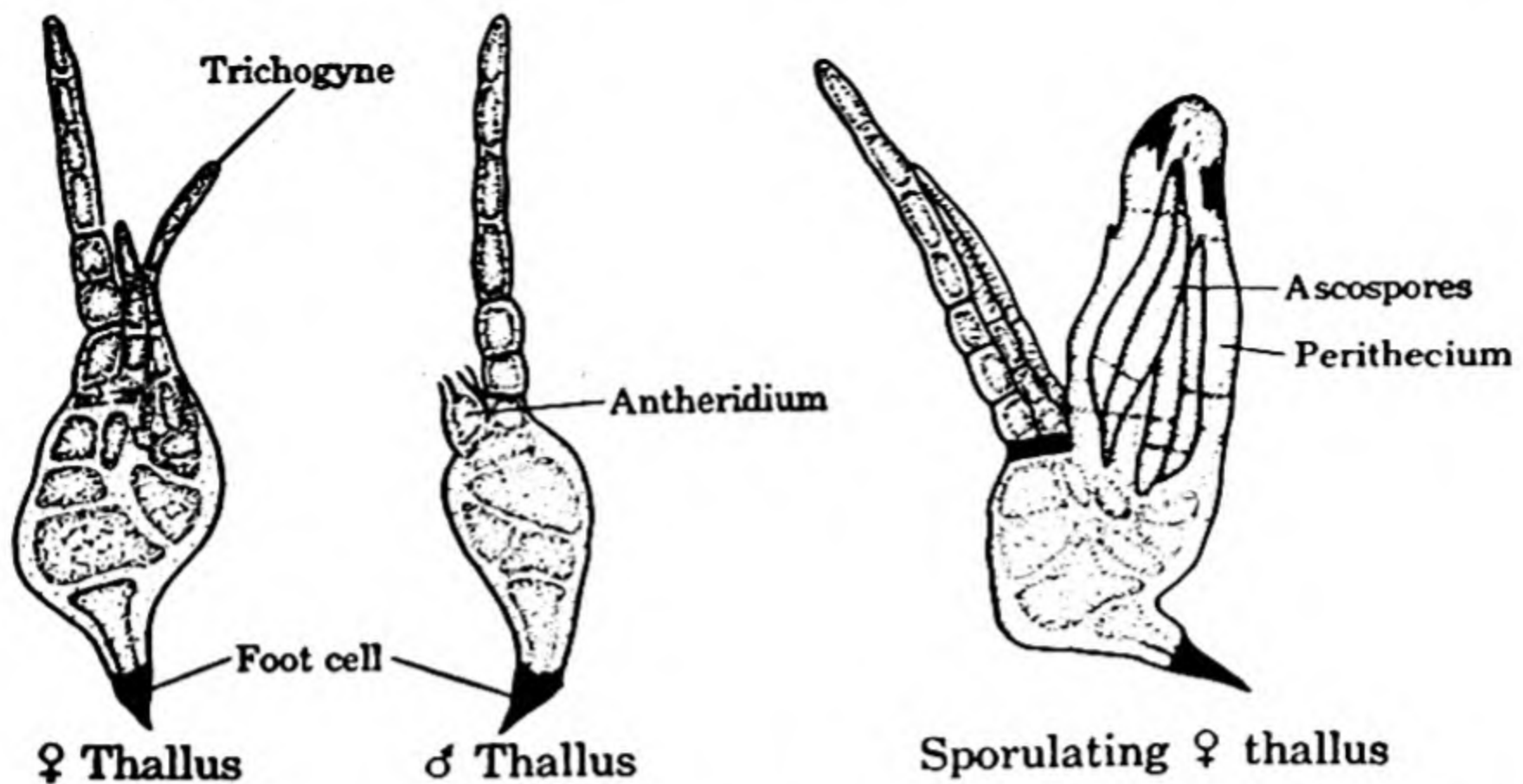


Figure 129. *Laboulbenia formicarum*. Redrawn from Benjamin and Shanor, 1950, *Am. Jr. Bot.*, 37:471-476.

taxonomic characters in the few instances in which cross-inoculations resulted in infection and complete thallus development.

In some Laboulbeniales, specialization becomes even more extreme. Not only are most forms specialized on a particular insect species, but also some of them attack only individuals of one sex, and these only on a particular spot of their body. Other species may attack the same insect, but are confined to a different portion of its anatomy. Such extreme specialization would seem fantastic and incredible were it not for the fact that reputable students of this group have verified it by repeated, careful observations.

Unfortunately, none of the Laboulbeniales has been grown on artificial media, and experimental work is not likely to be undertaken on a large scale with many species until this problem is solved. In the meantime, careful observations on living insects, such as those of Thaxter (1891-1931) and later of Benjamin and Shanor (1952), may give us some clues which will help explain such specialization.

The ascocarps of the Laboulbeniales are minute, stalked perithecia without paraphyses or paraphyses, containing four- to eight-spored asci. Sexual reproduction is by means of spermatization; non-motile sperm cells (spermatia) are released from male gametangia (antheridia) and spermatize the trichogynes of the ascogonia. R. K. Benjamin and Leland Shanor, in a paper (1950) on these interesting fungi, reported the discovery of dioecism in *Laboulbenia formicarum*. The sex organs in this species are segregated, the species consisting of

male and female individuals (Figure 129), a phenomenon which is not frequently observed in the Ascomycetes.

Asexual reproduction is not known to occur in the Laboulbeniales.

Of no economic importance whatsoever, the Laboulbeniales are nevertheless interesting because of their possible phylogenetic significance in accordance with the theory that the Ascomycetes have been derived from the red algae rather than from the Zygomycetes (Bessey, 1942, 1950; Dodge, 1914) and also because of their extreme specialization as parasites.

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17 sub-class LOCULOASCOMYCETIDAE the ascostromatic fungi

The sub-class Loculoascomycetidae was described by Lüttrell (1955) as Loculoascomycetes. The group corresponds to the Ascoloculares of Nannfeldt (1932). The name refers to the stromatic locules in which these fungi produce their asci.

Two characters are invariably linked in the fungi we place in this sub-class: (1) the asci are bitunicate (Figures 87E, 131B-G); (2) the ascocarps are ascostromata in which the asci are borne in locules. Some Euascomycetidae have bitunicate asci and some others bear unitunicate asci in ascostromata, but when the two characters (bitunicate ascus and ascostroma) are combined, we place the fungus in the Loculoascomycetidae.

Somatic Structures. The thallus of the Loculoascomycetidae cannot be distinguished from that of the Euascomycetidae in the light of our present knowledge. Whether or not there are important differences in microstructure remains for the electron microscope to reveal. The single extant study, that of Moore and McAlear (1962), revealed that the septa of *Pseudoplea gäumannii*, one of the Loculoascomycetidae, have the same structure as those of four Discomycetes which were studied.

Asexual Reproduction. A large number of Loculoascomycetidae produce conidia, but many do not, propagating solely by means of their ascospores. The conidial forms are varied, the same fungus sometimes producing two or perhaps more types which bear no resemblance one to the other. On the other hand, there appears to be a direct correlation between certain genera and the type of conidia they produce, so that, in these instances, we can predict fairly accurately the type of perfect or imperfect stage the fungus possesses if one or the other is known. As we have seen, this is true also of some genera of the Euascomycetidae (*Phyllactinia*, *Diaporthe*, etc.).

Sexual Reproduction. This also varies greatly, and no meaningful general statement can be made. Gametangial contact, spermatization, and somatogamy are all operative in these fungi. Some, no doubt, also reproduce apogamously, the ascal system originating from the female sexual apparatus without benefit of male.

The Ascocarp. As mentioned above, the ascocarp of the Loculoascomycetidae is an ascostroma. The ascogonia are always formed within a stroma whose structure may be either plectenchymatous or pseudoparenchymatous. After plasmogamy takes place, the growth and differentiation of the stroma develops the ascocarp, which consists of stromatic tissue surrounding the asci and of any sterile threads that may be present. Thus there is no special wall around the ascocarp centrum such as the perithecial wall of the stromatic Pyrenomycetes. There is only a cavity within the stroma in which the asci are located.

The stroma of the Loculoascomycetidae may be multilocular or unilocular. If unilocular it is extremely difficult to distinguish from a true perithecium unless its development is studied. Such a uniloculate ascostroma is often called a **pseudoperithecium** or a **pseudothecium** (Gr. *pseudo* = false + *theke* = box).

Luttrell distinguishes three types of ascocarp centrum in this group of fungi: the *Dothidea*, the *Pleospora*, and the *Elsinoe*. In all three types, the ascogonia typically originate in a plectenchymatous or pseudoparenchymatous stroma.

In the *Dothidea* type the locules are delimited around the ascogonia, and the asci, originating at a single point, push up into the pseudoparenchyma of the locule and spread out like a fan. Either a pore is dissolved in the stroma over the mature asci, or an ostiole with periphyses develops. No sterile threads of any sort develop among the asci.

In the *Pleospora* type vertical sterile hyphae—the pseudoparaphyses—originate in the stroma where the ascogonium is located. A locule then develops in this region around the ascogonium and pseudoparaphyses, possibly caused by pressure exerted by the latter. Asci now develop among the pseudoparaphyses and grow upward between them. A pore is dissolved in the stroma above the mature asci.

In the *Elsinoe* type, ascogenous hyphae developing from the ascogonium spread out into the stroma and develop asci individually. A locule is formed around each ascus. The monascous locules are thus often scattered, but a fertile region may become differentiated in the stroma and the locules may be developed in a single layer.

Classification. Luttrell (1955) recognizes six orders in the Loculoascomycetidae: Myriangiales, Dothideales, Pleosporales, Microthyriales, Hysteriales, and Trichothyriales. The last one, however, is included as a family (Trichothyriaceae) in the Microthyriales by Martin (1961). The five orders we shall recognize may be separated in accordance with the following simple key:

SIMPLE KEY TO THE ORDERS OF THE SUB-CLASS LOCULOASCOMYCETIDAE

- | | |
|--|-----------------------|
| A. Locules uniascal; usually scattered at various levels in the ascostroma | <i>Myriangiales</i> |
| AA. Locules generally polyascal; arranged in a basal layer | |
| B. Stroma flattened, dimidiate ¹ | <i>Microthyriales</i> |
| BB. Stroma not flattened | |
| C. Stroma boat-shaped, opening by a longitudinal slit | <i>Hysteriales</i> |
| CC. Stroma not boat-shaped | |
| D. Pseudoparaphyses present | <i>Pleosporales</i> |
| DD. Pseudoparaphyses lacking | <i>Dothideales</i> |

¹ The two halves very unequal or one-half lacking altogether.

order MYRIANGIALES

The Myriangiales comprise a small group of stromatic Ascomycetes parasitic on plants or insects in the tropics or in the temperate zones. We know so little about the Myriangiales that their taxonomy is in a state of confusion. Mycologists differ as to the families and genera which they include in this order. There is rather general agreement on the inclusion of the Myriangiaceae and the Elsinoeaceae in the Myriangiales, but some authors combine these two families under the name Myriangiaceae. In 1956, Ciferri, Batista, and Campos described the family Piedraiaceae, which they placed in this order.

family ELSINOEACEAE

The Elsinoeaceae include the single genus *Elsinoe*, consisting of a number of important plant pathogens, among which are *Elsinoe fawcetti*, the cause of citrus scab; *Elsinoe ampelina*, the cause of grape anthracnose; *Elsinoe veneta*, the cause of raspberry anthracnose; and *Elsinoe perseae*, which attacks the avocado.

Burkholder (1917) investigated the life cycle of *Elsinoe veneta* in its gross aspects. This species may serve as our example of this

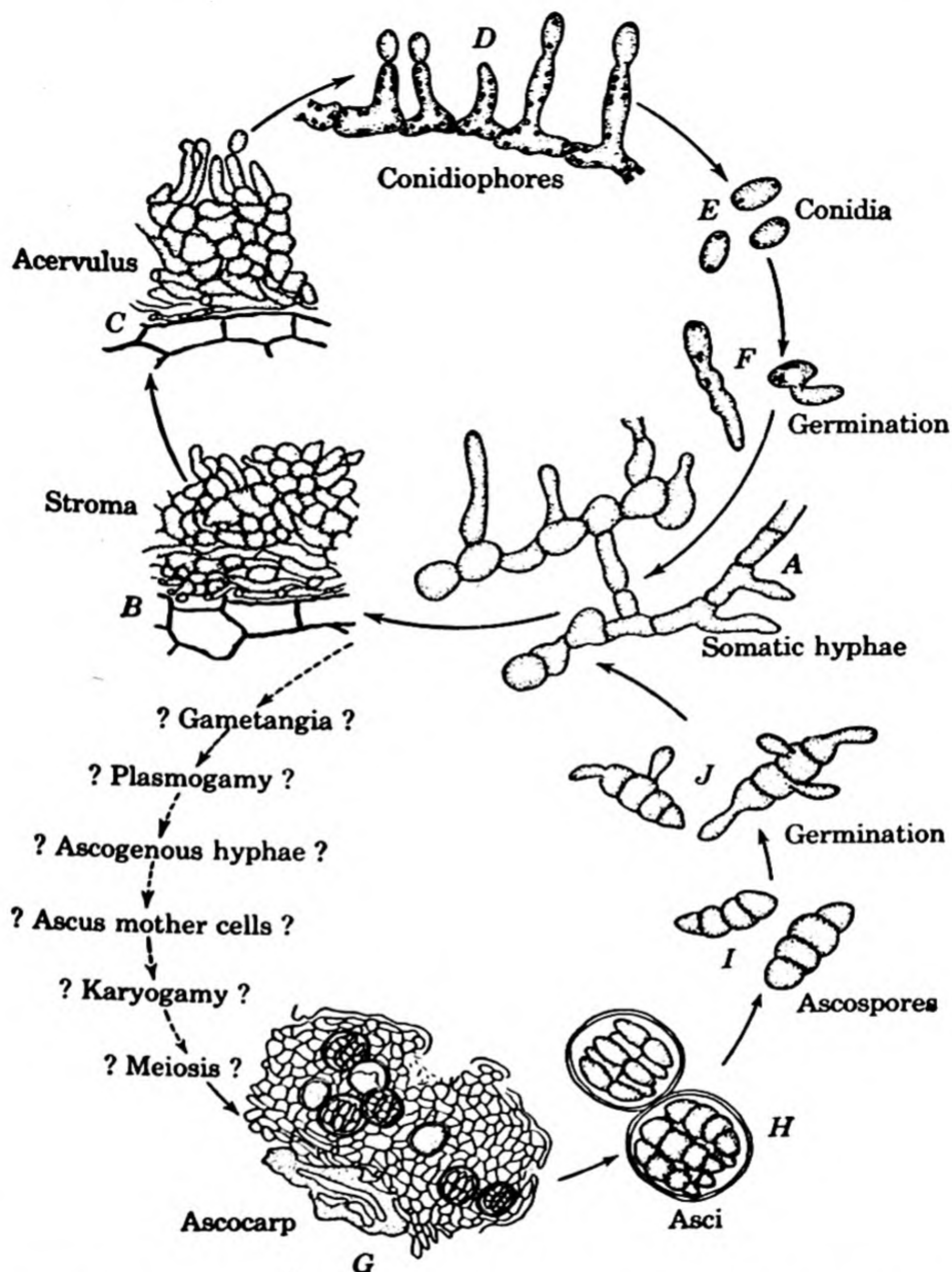


Figure 130. Life cycle of *Elsinoe veneta*. Redrawn from Burkholder, 1917, *Cornell Univ. Agr. Exp. Sta. Bull.*, 395:157-183.

group (Figure 130). The four-celled hyaline ascospores mature in late fall or, more often, in early spring, within the globose asci which are borne singly within cavities scattered in the stromatic ascocarp. As the upper portion of the stroma weathers away and the asci are exposed, their inner walls elongate greatly when wet, burst, and expel the ascospores forcibly. The ascospores are covered with a gelatinous substance which enables them to stick to a solid surface and await favorable conditions for germination. When covered with a film of water, the ascospores produce short sterigmata on which conidia are borne. These germinate by germ tubes which cause infection if the ascospores happen to be lying on the surface of a susceptible host, such as various species of *Rubus*. The mycelium, resulting from conidial germination, forms a small subcuticular stroma on which an acervulus produces conidia borne on short conidiophores. The conidia, like the ascospores, are embedded in a gelatinous matrix. The asexual cycle of the fungus repeats itself throughout the spring and summer, spreading the disease from plant to plant. In late summer, the ascigerous stromata are formed, and the fungus passes the winter in this stage. Cytological details are lacking.

All species of *Elsinoe* discovered thus far possess the same general type of imperfect stage which is referred to the form-genus *Sphaceloma* of the Deuteromycetes.

family MYRIANGIACEAE

Millardet (1868), Petch (1924), Tai (1931), and Miller (1938) investigated the genus *Myriangium* in the Myriangiaceae. The stromata in this genus are generally cushion-shaped, and the ascocarps, which are extensions of the stroma, cover the upper part of the cushion. Each ascocarp resembles a more or less rigid, pseudoparenchymatous cup filled with softer tissue in which the asci are scattered irregularly (Figure 131). As in *Elsinoe*, the tissue in which the asci are embedded weathers away, and the asci become exposed. When wet they absorb water, swell to two or three times their size, and expel the multicellular ascospores. The genus *Myriangium* includes a number of species parasitic on insects.

In his investigations of *Myriangium duriaei* and *Myriangium curtissii* on scale insects in Georgia, Miller found ascogonial coils associated with what he believed may be antheridial coils, but has observed no plasmogamy. It is therefore uncertain whether the paired nuclei which he found in the ascogonia are the result of plasmogamy

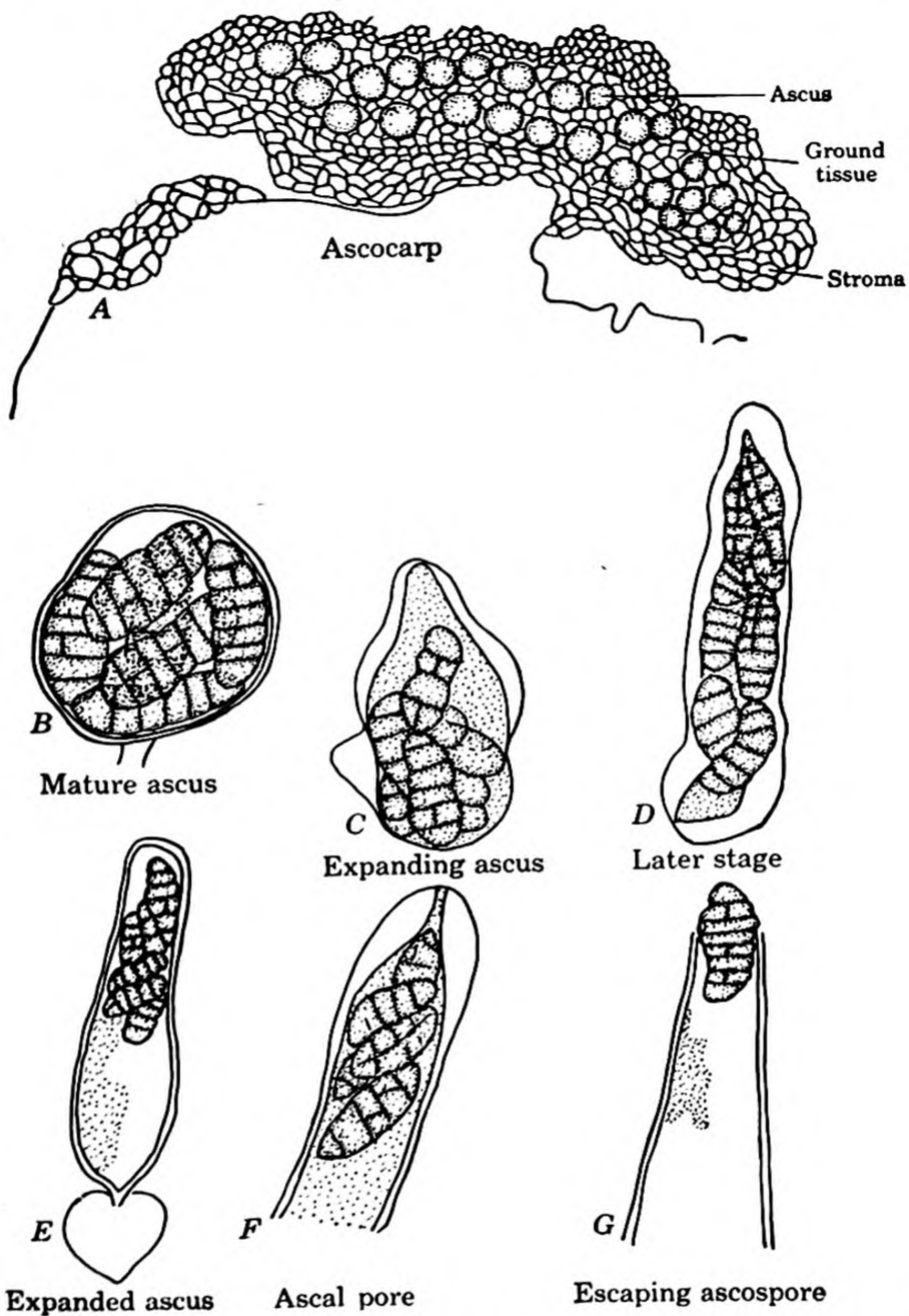


Figure 131. *Myriangium bambusae*. Redrawn from Tai, 1931, *Sinensia*, 1:147-164.

or whether they represent the pairing of ascogonial nuclei. The tissue surrounding the cavities in the center of the ascocarp is composed entirely of ascogenous hyphae from which the ascus mother cells originated.

family PIEDRAIACEAE

The family Piedraiaceae consists of the genus *Piedraia*, which is based on *Piedraia hortai*, probably the only species (Ciferri, Batista, and Campos, 1956). *Piedraia hortai* is parasitic on human hair, causing "black piedra." The stroma of the fungus forms around a hair. It contains many uniascal locules, arranged usually in one layer. The asci are globose. Whether they are bitunicate has not been reported, to my knowledge. The ascospores are elongated, non-septate, and hyaline, and bear two flagellum-like appendages, one at each end. *Piedraia hortai* is a tropical fungus, distributed chiefly in South America, Java, and Cochin China (Beneke, 1957). The genus *Piedraia* is placed in the Microthyriaceae by Langeron and Vanbreuseghem (1952).

order DOTHIDEALES

The order Dothideales is based on the *Dothidea* type centrum described earlier. The chief characteristics of this order, therefore, are (1) the absence of interascal threads of any sort in the locule, and (2) the formation of bitunicate asci, usually in fascicles, which push through the stromatic tissue during their development and dissolve cavities around them.

A large number of the Dothideales are tropical, but some occur widely in the temperate zones. The order is subdivided into four families: Dothideaceae, Dothioraceae, Pseudosphaeriaceae, and Capnodiaceae. Not all authors agree on this classification, but then you should begin to suspect by now that there are few points of agreement on almost any question concerning the classification of the Ascomycetes!

family DOTHIDEACEAE

This is a large family of universally distributed fungi. *Mycosphaerella* is the largest genus in this family, with over 1000 described species. Although the majority of these are saprobic, many are parasites of economic plants. Examples are *Mycosphaerella cercidicola*, which causes a leaf spot of redbud; *Mycosphaerella fragariae*, which

causes a very common leaf spot of strawberry; *Mycosphaerella sentina*, which causes leaf spot of pear; and *Mycosphaerella musicola*, the cause of the extremely destructive Sigatoka disease of bananas (Calpouzos, 1955).

The conidial stages of *Mycosphaerella* are varied. Some species produce their conidia in pycnidia, some in acervuli, and some on free conidiophores; other species do not possess conidia at all. Suffice it to say that there is no way of predicting the imperfect stage of an unidentified species of *Mycosphaerella* by inspecting its perfect stage alone.

In many species of *Mycosphaerella*, plasmogamy is probably accomplished by means of spermatization. What are probably spermatia (no one has been able to germinate these structures) have been discovered in a large number of species of this genus and related genera, and the evidence is very strong that they are actually functional male organs (Higgins, 1920, 1929, 1936; Jenkins, 1939; Wolf, 1943).

In general the spermatia of *Mycosphaerella* are borne in spermogonia (sing. spermogonium; Gr. *sperma* = seed, sperm + *gennao* = I give birth) which resemble pycnidia and have often been mistaken for a conidial stage of these fungi. Such spermatia are formed in basal spermogonial cells and are pushed out through a sterigma-like protuberance of the parent cell. They are rod-shaped and minute, measuring around $1\ \mu$ by $3\ \mu$.

Higgins (1936) showed that in *Mycosphaerella tulipiferae* the spermatia are in all probability functional male cells. He saw spermatia fused with the tips of trichogynes (Figure 132F) and also found empty spermatial walls still attached to trichogynes containing a distinguishable spermatial nucleus in addition to their own. The life history diagram (Figure 132), constructed from Higgins' excellent drawings, will show you how the ascocarp cavity is dissolved within the stroma by the growing tuft of asci. This arrangement of the asci (Figure 132L) is typical of the Dothideales.

Barr (1958), studying *Mycosphaerella tassiana* and *Mycosphaerella typhae*, found no typical ascogenous hyphae. A number of multinucleate cells develop at the base of the locule. Each develops a protrusion into which two nuclei pass. This cell may become crozier-like or may develop directly into an ascus by enlarging. Karyogamy and meiosis take place before spores are formed.

Various species of *Mycosphaerella* are relatively easy to culture, but most of them produce only the conidial stage on artificial media. Barr (1958) in her study of *Mycosphaerella tassiana* found that,

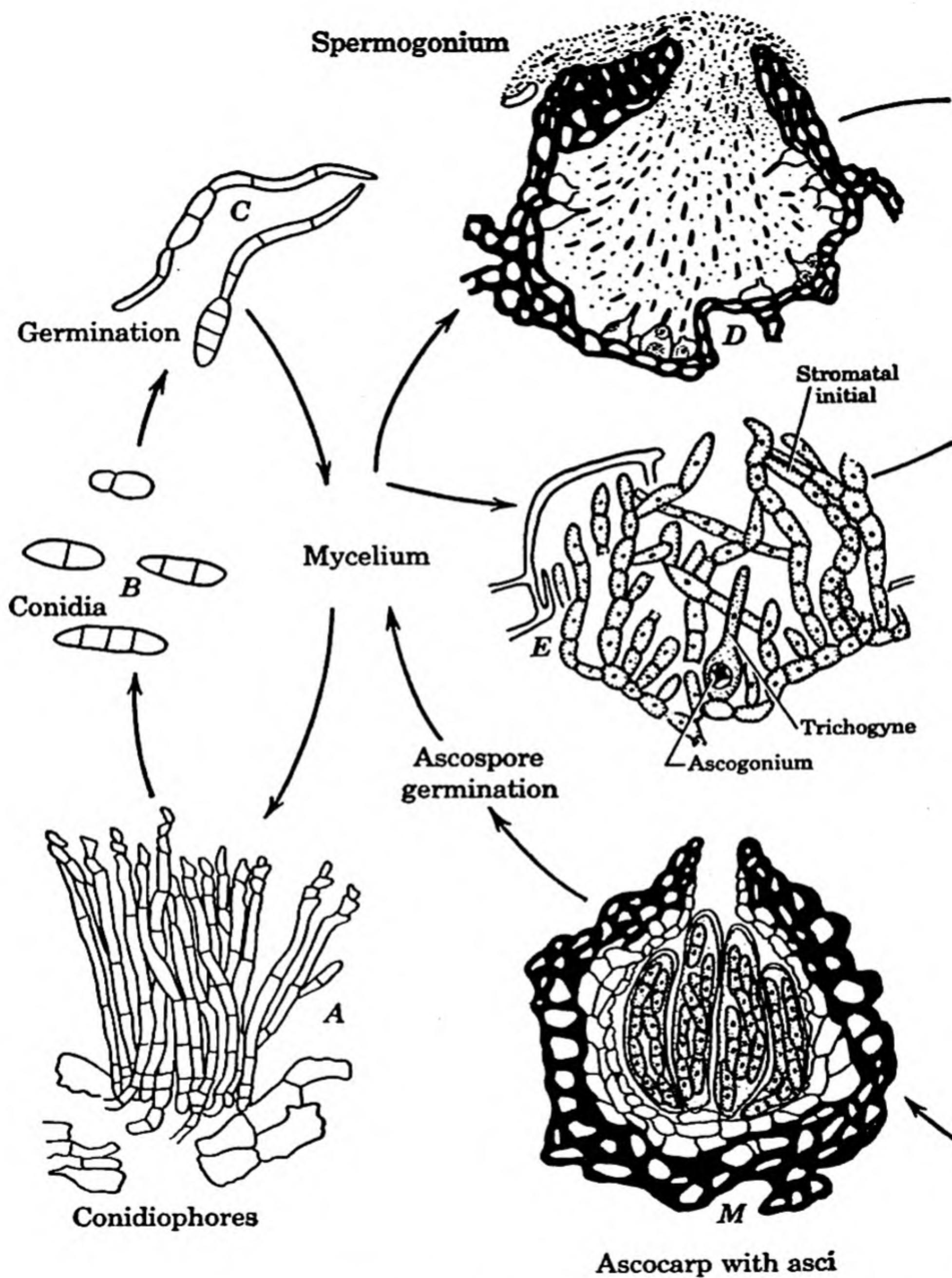
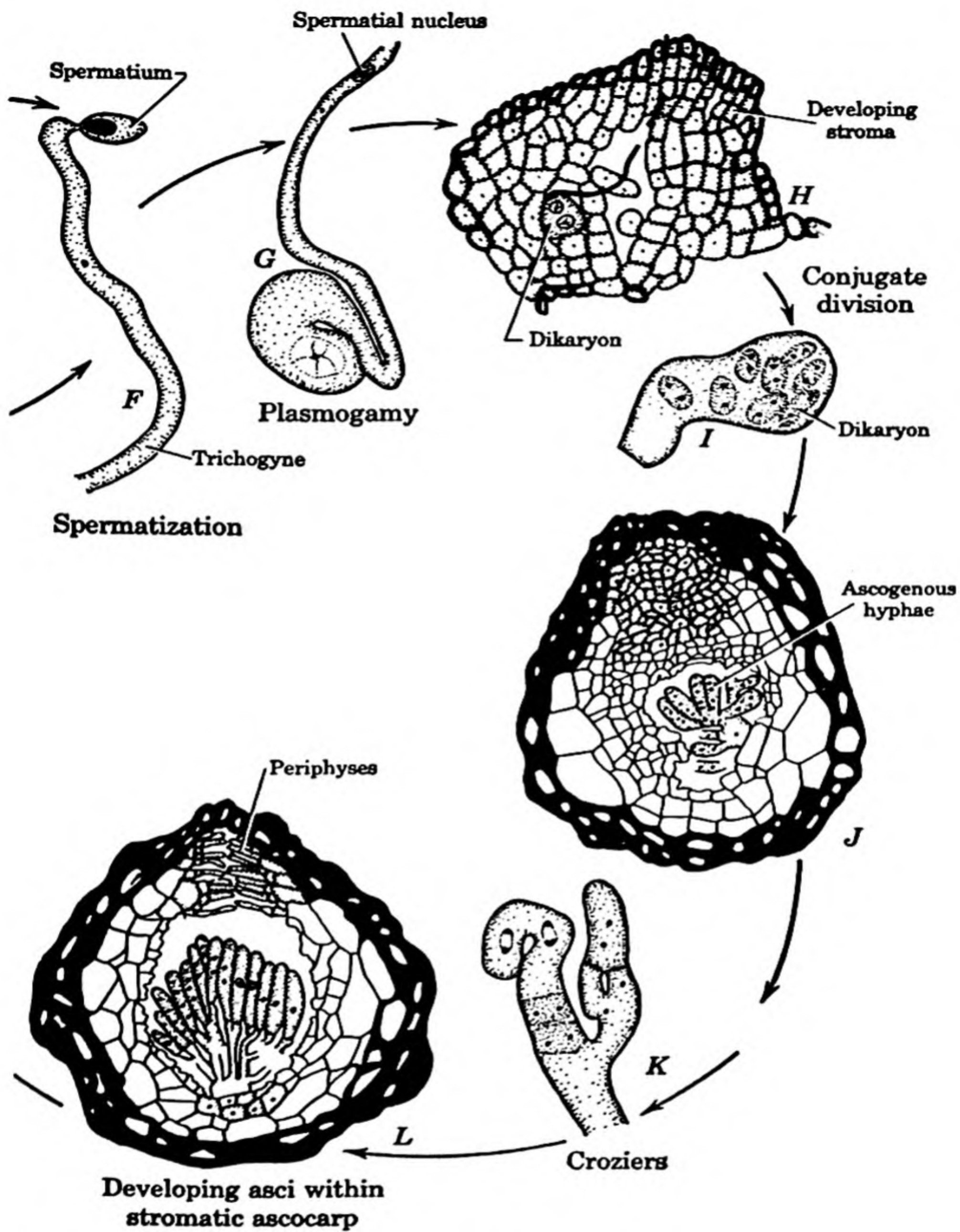


Figure 132. Life cycle of *Mycosphaerella tulipiferae*.



Redrawn from Higgins, 1936, *Am. Jr. Bot.*, 23:598-602.

unless the cultures were exposed to low temperatures, no ascostromata are formed, and furthermore, unless the cold-temperature treatment was prolonged for at least 6 weeks, no sporulation took place. On the contrary, *Mycosphaerella typhae* produced mature asci without cold treatment. It is interesting to note that *Mycosphaerella tassiana* is chiefly an arctic or alpine species, whereas *Mycosphaerella typhae* occurs in the temperate zones.

Another important and large genus in the Dothideaceae is *Guignardia*. It differs from *Mycosphaerella* in that its ascospores are usually unequally two-celled, whereas those of *Mycosphaerella* are clearly two-celled. *Guignardia bidwellii* attacks the grape (genus *Vitis*) and members of the related genus *Parthenocissus*, to which the Boston ivy (*Parthenocissus tricuspidata*) and the Virginia creeper (*Parthenocissus quinquefolia*) belong. Investigations by Luttrell (1948) showed that, although the fungus is morphologically similar on these hosts, it is nevertheless biologically specialized so that the form on *Parthenocissus* will not attack *Vitis* and *vice versa*. The life history of this fungus has been studied by a number of investigators, particularly by Reddick in the United States and by Viala and Ravaz in France. The fungus, a native of North America, was exported into France accidentally and became a serious parasite on the European grape.

Guignardia bidwellii forms a mycelium which grows in the host tissues and kills a number of cells, causing large dead spots on the leaves. On the berry the infected spot enlarges rapidly, enveloping the entire berry within a few days and converting it into a mummy. On the leaf spots as well as on the infected fruit the fungus soon forms pycnidia (*Phyllosticta labruscae*) (Figure 133A), which are characteristically arranged in a circular zone. These contain numerous, large, oval pycnidiospores (conidia) which exude from the pycnidial pore. The conidia germinate easily and form germ tubes (Figure 133C), which infect the host. In addition to the pycnidia the fungus forms spermogonia containing minute, bacillus-shaped spermatia (Figures 133E, F). These do not germinate. Presumably they act as male cells in spermatization, but this remains to be proved.

Guignardia bidwellii produces two types of uniloculate stromata besides the spermogonia. Both are globose with a pore at the top. One type, the pycnosclerotium (Figure 133D), when crushed gives forth a considerable amount of oil in the form of small droplets, but contains no spores of any kind. Reddick (1911) thought that pycnosclerotia develop into ascocarps, but Caltrider (1961) reported that they produce conidia after a prolonged period of incubation. The

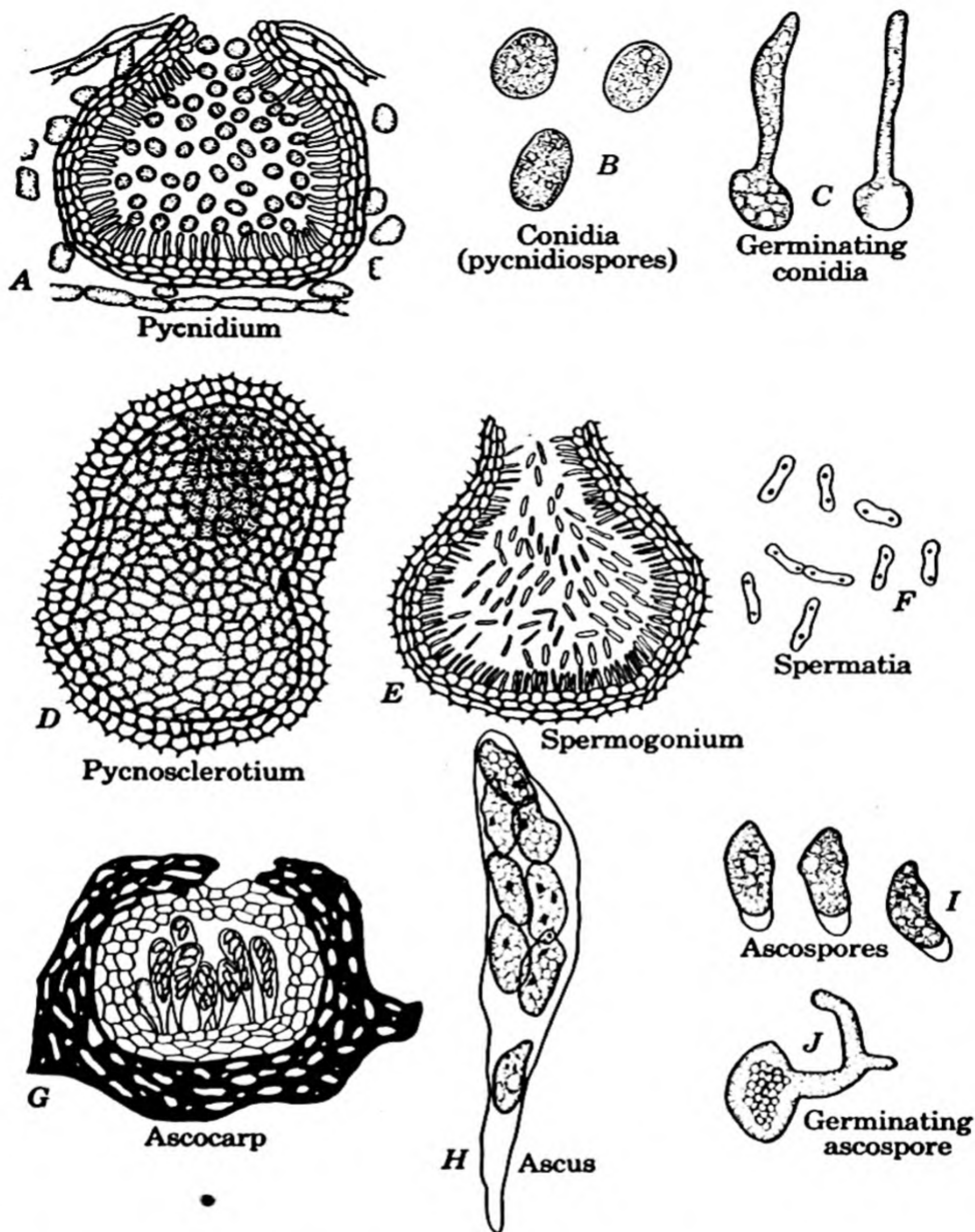


Figure 133. *Gutgnardia bidwellii*. C-J, redrawn from drawings and photographs from Reddick, 1911, *Cornell Univ. Agr. Exp. Sta. Bull.*, 293:289-364.

second type of stroma resembles the pycnosclerotium, but is actually an ascocarp (Figure 133G) containing asci, with eight ascospores. Whether or not these two structures represent two stages of a developing ascocarp remains to be worked out. The ascospores of this fungus are very unequally two-celled (Figure 133I); the basal cell gives the appearance of a very short stalk and is apparently sterile.

Other genera belonging to this family about which we have considerable information are *Dothidea* (Luttrell, 1951a), *Systremma* (Luc, 1952), and *Dothidella* (Hess and Müller, 1951). Chadeffaud's remarks (1954) on the asci of *Systremma natans* and *Bertia moriformis* are of interest in relation to the whole question of ascus structure and classification.

family PSEUDOSPHAERIACEAE

The ascostroma of the Pseudosphaeriaceae is a pseudothecium in which the asci are formed singly within the ascocarp and remain separated by stromatal tissue. In this respect the family resembles the Myriangiales, and, as Luttrell (1955) states, it appears to be intermediate between this order and the Dothideales. The development of *Pseudoplea gäumannii* (Müller, 1951; Wehmeyer, 1955a) strikingly resembles that of some species of *Mycosphaerella* (see Barr, 1958).

The Dothioraceae are probably closely related to the Pseudosphaeriaceae. They differ chiefly in that the asci form a closely packed palisade layer rather than arising singly. For a full discussion of these fungi see Müller and von Arx (1950).

family CAPNODIACEAE

These are the sooty molds, abundant in tropical and warmer subtropical climates and in northern greenhouses, and usually associated with insect secretions on the surface of living plants. They are only rarely parasitic on the plants, most species growing entirely superficially, but growth is often so abundant that they injure the plants by significantly reducing the photosynthetic area.

The systematic position of the Capnodiaceae continues to be in dispute, and the family is constantly being transferred from order to order. As Luttrell (1951b) points out, we do not know whether the asci are actually bitunicate. The placement of the Capnodiaceae in the Dothideales is based on Fraser's (1935) developmental study,

which is unique for this group of fungi. The individual ascostromata resemble perithecia in external appearance when produced singly. Often, however, they are branched and lobed.

There is a great need for both morphological and physiological study in the Capnodiaceae.

order PLEOSPORALES

As now delimited, the Pleosporales are characterized by the *Pleospora* type centrum, in which the asci develop among pseudoparaphyses and grow upward between them. Pseudoparaphyses, you will remember, are attached both to the roof and the floor of the locule. They originate in the upper wall and grow downward. The ascostroma is either a pseudothecium or a multiloculate cushion-shaped stroma.

We have seen in the previous order that in the Pseudosphaeriaceae the asci arise individually and dissolve cavities in the stroma. The cavities are separated by stromatal tissue which *remains* between them. In the Pleosporales, the sterile threads between the asci are not remnants of stromal tissue but pseudoparaphyses which originate *before the formation of the asci*.

This is a very difficult distinction to make in a mature ascostroma and has led to misinterpretation of structures and consequently to differences in classification.

The order is subdivided into seven families by Luttrell (1955). We shall discuss only the Venturiaceae and shall mention the Pleosporaceae and Lophiostomataceae.

family VENTURIACEAE

The Venturiaceae are plant parasites which produce their ascostromata subepidermally or subcuticularly. Conidiophores are often developed from such stromata and push through to the surface, where they produce their conidia. The ascostromata vary somewhat with the different genera and species. Some are glabrous, but the majority perhaps bear hairs or setae, particularly around the pore, dissolved over the mature asci. When the pore is formed, the pseudoparaphyses absorb water, gelatinize, and fill the pore. The ascospores are two-celled, ovoid or ellipsoid. At first colorless or pale green, they change to olive-brown or grayish green, rarely dark brown at maturity.

Venturia is the largest and most important genus in this family. It includes a number of serious parasites, such as *Venturia inaequalis*, the cause of apple scab, and *Venturia pyrina*, the cause of pear scab. *Gibbera*, *Stigmatea*, and *Parodiella* are among the other genera in this family. Von Arx (1952) gives a key to the genera of the Venturiaceae and briefly characterizes each genus.

Venturia inaequalis (Cke.) Wint.

Venturia inaequalis attacks the apple, crab apple, hawthorn, various ornamentals of the genus *Malus*, the loquat (*Eriobotrya japonica*), and other plants. It infects the leaves, fruits, and young twigs of the host, and causes severe damage by reducing the quality of the fruit and by weakening the host through defoliation. The fungus is universally distributed in all apple-growing sections of the world and is considered one of the most important parasites of the apple.

In the spring at the time the apple buds are bursting, the fungus begins its life cycle by forcibly ejecting its ascospores through the openings of ascocarps buried in the tissues of dead apple leaves lying on the ground. Weather conditions which favor the development of the apple buds also favor the development of the ascospores of this fungus, so there is a definite correlation between the two. The ascospores are two-celled, yellowish, with the upper cell shorter and somewhat wider than the lower (Figure 134H). The unequal size of the two cells of the ascospore gives the species its name. Air currents lift the ascospores to the apple leaves on the trees, and in the presence of moisture germination occurs (Figure 134I).

The germ tubes issuing from the ascospores penetrate the cuticle, and the mycelium begins to grow, forming a thin, subcuticular stroma. A few days after infection, numerous short conidiophores (Figure 134B) break through the cuticle and each produces a flame-shaped conidium at the tip, so that conidiophore and conidium resemble a short burning candle. The conidial stage of *Venturia inaequalis* is named *Spilocaea pomi* in accordance with the convenient custom, now legalized by the International Rules of Botanical Nomenclature, of using the name of the form-genus and species to designate the imperfect stage of a fungus (see Chapter 18 for a full explanation).

Each conidiophore cuts off successively a number of conidia at its tip, the conidiophore elongating after each conidium is produced. The conidia are generally one-celled, but often they become two-celled through septation. At maturity they are smoky brown. Co-

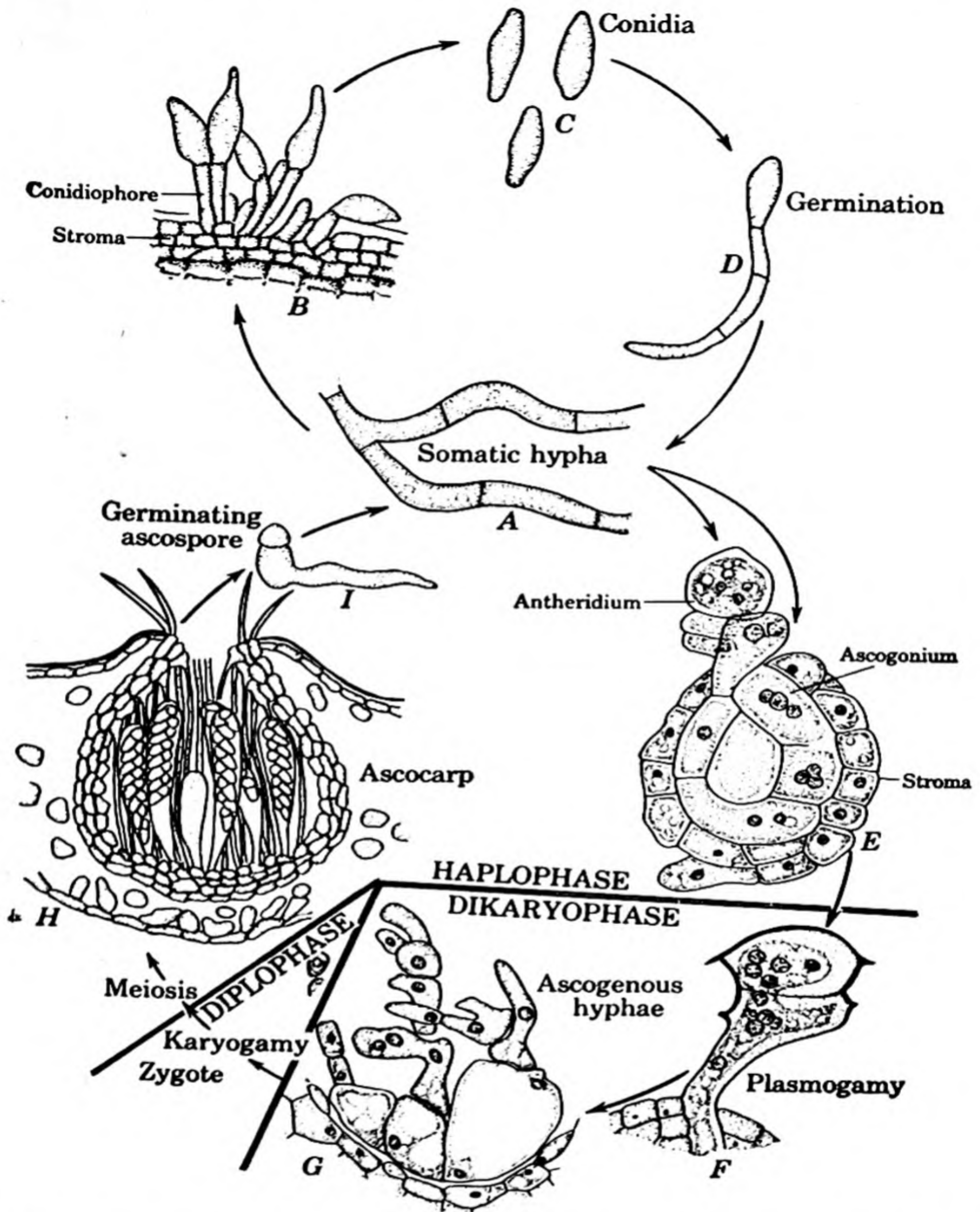


Figure 134. Life cycle of *Venturia inaequalis*. The fungus is heterothallic, requiring two compatible mating types for sexual reproduction. E–G, redrawn from Killian, 1917, *Zettschr. Botanik*, 9:353–398.

nidia are spread by rain to other leaves or to young fruits in various stages of development, which they soon infect by means of germ tubes issuing from the ends or from the sides of the conidium. The fungus propagates itself asexually throughout the spring and summer, producing several conidial generations.

Late in the season when the leaf cells begin to die, the mycelium penetrates deep into the leaf tissues and proceeds to form ascocarps as follows. A small coil in a hypha consisting of uninucleate cells initiates the formation of the stroma. As this develops, a coil of multinucleate cells representing the ascogonium differentiates inside the young stroma, and a trichogyne pushes through and protrudes from the stomatal wall (Figure 134E). In the meantime, an antheridium is formed from a hypha of the opposite strain and contact is soon established between the antheridium and the trichogyne. Keitt and Palmiter (1938) showed that *Venturia inaequalis* is heterothallic. The ascogonium and antheridium must originate from individuals belonging to different strains before plasmogamy can take place. Through pores dissolved in the gametangial walls at the point of contact, the antheridial nuclei pass into the ascogonium through the trichogyne (Figure 134F) and pair with the ascogonial nuclei. The nuclear pairs pass into the ascogenous hyphae, which now develop from the lower portion of the ascogonium (Figure 134G). Ascus formation takes place by the formation of croziers in the usual manner. In the meantime, the stroma continues to develop and forms the ascocarp (Figure 134H). Development of the ascocarp, asci, and ascospores proceeds very slowly throughout the late fall, winter, and early spring, the rate of development being regulated by such factors as temperature and moisture. The ascospores mature in April or May, depending on the locality, and are forcibly ejected through an opening which forms in the ascocarp above the asci.

The pathogenicity, epidemiology, and genetics of *Venturia inaequalis* have been studied extensively over a long period of years at the University of Wisconsin under the direction of Professor Keitt.

family PLEOSPORACEAE

It is impossible at present to define this family for you. Until we learn more about the characteristics of the Pleosporales as a whole, the limits of the genera and families are bound to be very vague. As now described (Luttrell, 1951, as Pseudosphaeriaceae), the family is obviously heterogeneous. Several mycologists are investigating

various genera in this family, and different developmental lines will eventually be sorted out. The work of Wehmeyer (1949 and subsequent) in the United States on *Pleospora* and other genera, that of Müller (1950) in Switzerland, and that of Holm (1957) in Sweden are among the most comprehensive studies of the Pleosporaceae.

The Pleosporaceae at present include a number of large and important genera, such as *Leptosphaeria*, *Pleospora*, *Cochliobolus*, *Ophiobolus*, and *Cucurbitaria*, some of which cause severe plant diseases.

family LOPHIOSTOMATACEAE

The ascocarp of the Lophiostomataceae has the general appearance of a perithecium with a prominent neck laterally compressed and provided by a narrow slit through which the ascospores escape. Beyond this, we know nothing about the structure of these fungi. The assumption is that the ascocarp is a pseudothecium and that it has the *Pleospora* type centrum, but this is only conjecture.

OTHER ORDERS OF LOCULOASCOMYCETIDAE

In addition to the orders already discussed, the Loculoascomycetidae include the Microthyriales and Hysteriales.

The Microthyriales have a shield-shaped, dimidiate ascostroma with a *Pleospora* type centrum (Figure 135). The vast majority of these fungi are tropical. The order, sometimes called Hemisphaeriales, is divided by Luttrell into two families: Microthyriaceae and

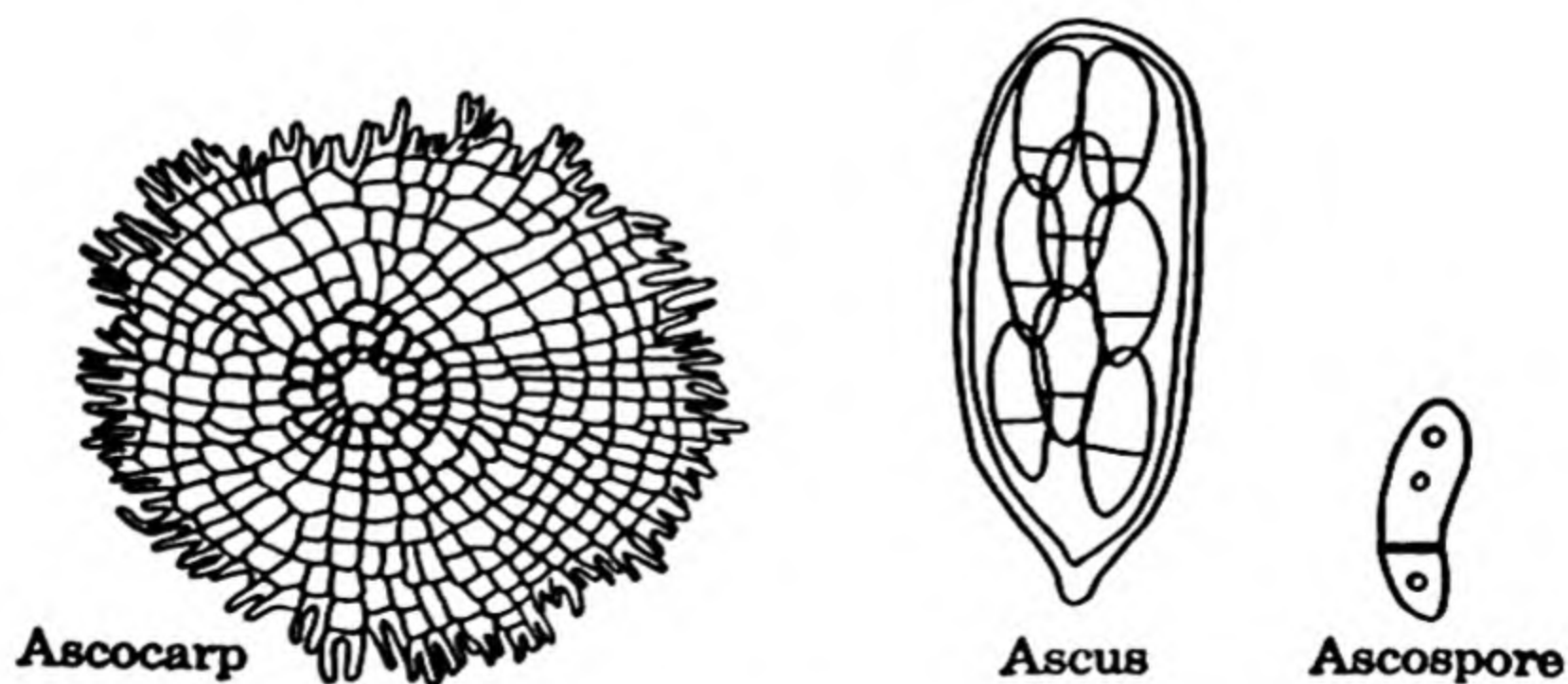


Figure 135. Microthyriales—*Microthyrium microscopium*. Redrawn from Saccardo, in Rabenhorst's *Kryptogamen Flora*, 1887, Vol. II, E. Kummer, Leipzig.

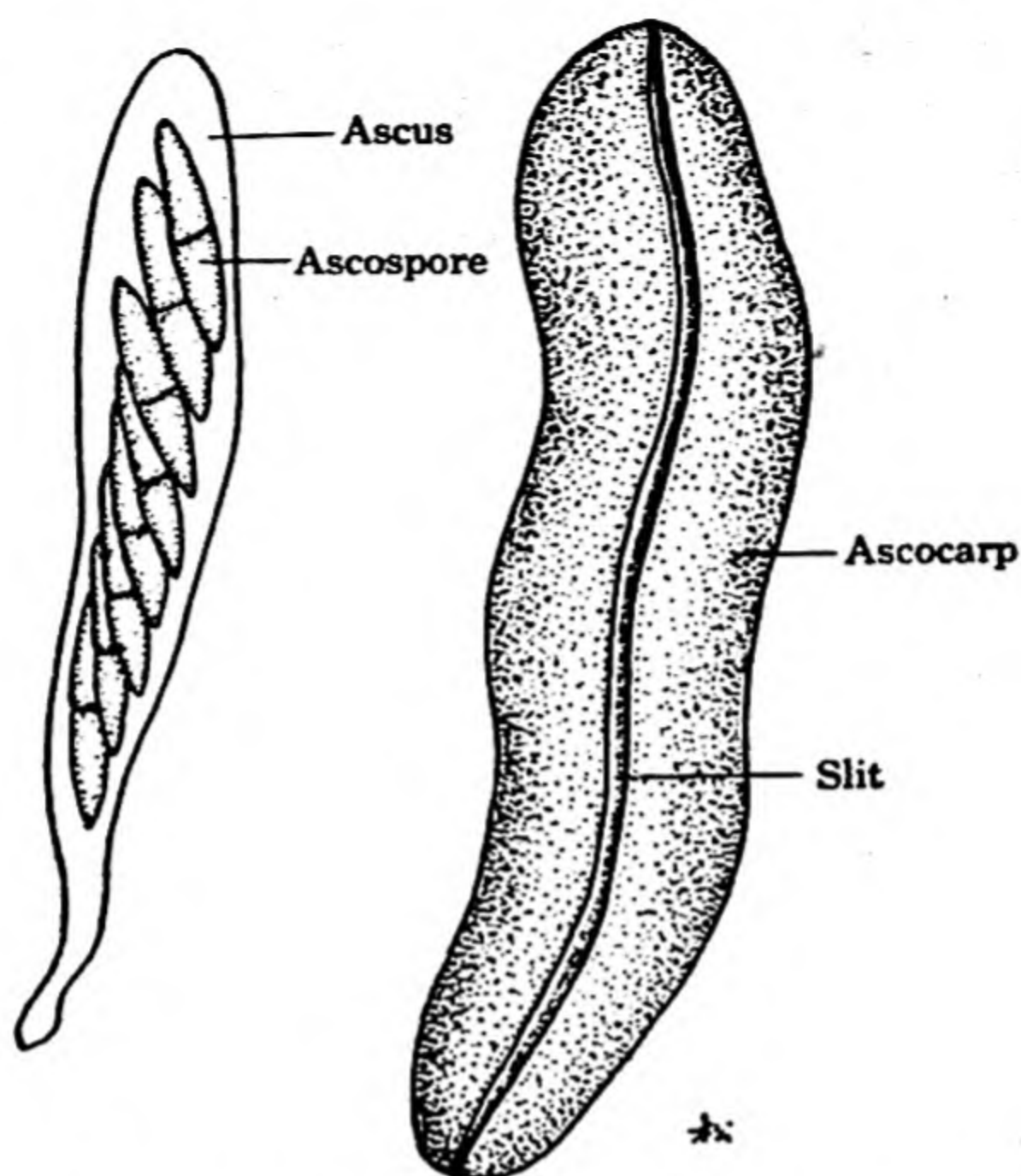


Figure 136. Hysteriales—ascocarp and ascus of *Glonium* sp.

Micropeltaceae. Both of these have been monographed, the first by Stevens and Ryan (1939), and the second by Batista (1959).

The Hysteriales are characterized by black, carbonous or leathery, boat-shaped or branched ascocarps, each with a long slit-like opening parallel to the long axis and extending almost through the entire length of the fruiting body (Figure 136). Some authors consider this type of ascocarp an intermediate between a perithecium and an apothecium. Bessey (1950) refers to this ascocarp as an apothecium and discusses these fungi with the Discomycetes. However, the bitunicate asci of the few forms which have been investigated, coupled with the presence of pseudoparaphyses (*Pleospora* type centrum), show that the relationships of the Hysteriales are with the Loculoascomycetidae rather than with the Discomycetes.

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18 form-class DEUTEROMYCETES the imperfect fungi

Introduction. A great many fungi are known which have septate mycelium and which, so far as anyone has been able to discover, reproduce only by means of conidia. Since these fungi apparently lack a sexual phase (perfect stage), we call them, commonly, imperfect fungi and, technically, Fungi Imperfecti. Many of these are saprobic, but many are of great importance to us because they are parasites which cause diseases of plants, animals, and human beings.

The conidial stages of most of these fungi are very similar to conidial stages of some well-known Ascomycetes, and we presume that, with relatively few exceptions, the imperfect fungi represent conidial stages of Ascomycetes whose ascigerous stages either are rarely formed in nature and have not been found, or have been dropped from the life cycle in the evolution of these organisms. Indeed, in some cases we have found the sexual stages in nature or have produced them in culture many years after the fungi were first described as imperfect fungi. In such cases, the organisms can be classified in the ascomycete genera in which the characters of the ascigerous stage place them. In a few cases, the perfect stages which have been discovered have proved to be Basidiomycetes. *We may consider the Fungi Imperfecti, therefore, as conidial stages of Ascomycetes or, more rarely, Basidiomycetes, whose sexual stages have not been discovered or no longer exist.* Nevertheless, with the discovery of a parasexual cycle which operates in many if not all of these fungi and offers them some of the advantages of sexuality, it is not at all inconceivable that some of the Deuteromycetes have never had a perfect stage.

Somatic Structures. With the exception of the thallus of the asporogenous yeasts (page 408), the thallus of the Fungi Imperfecti

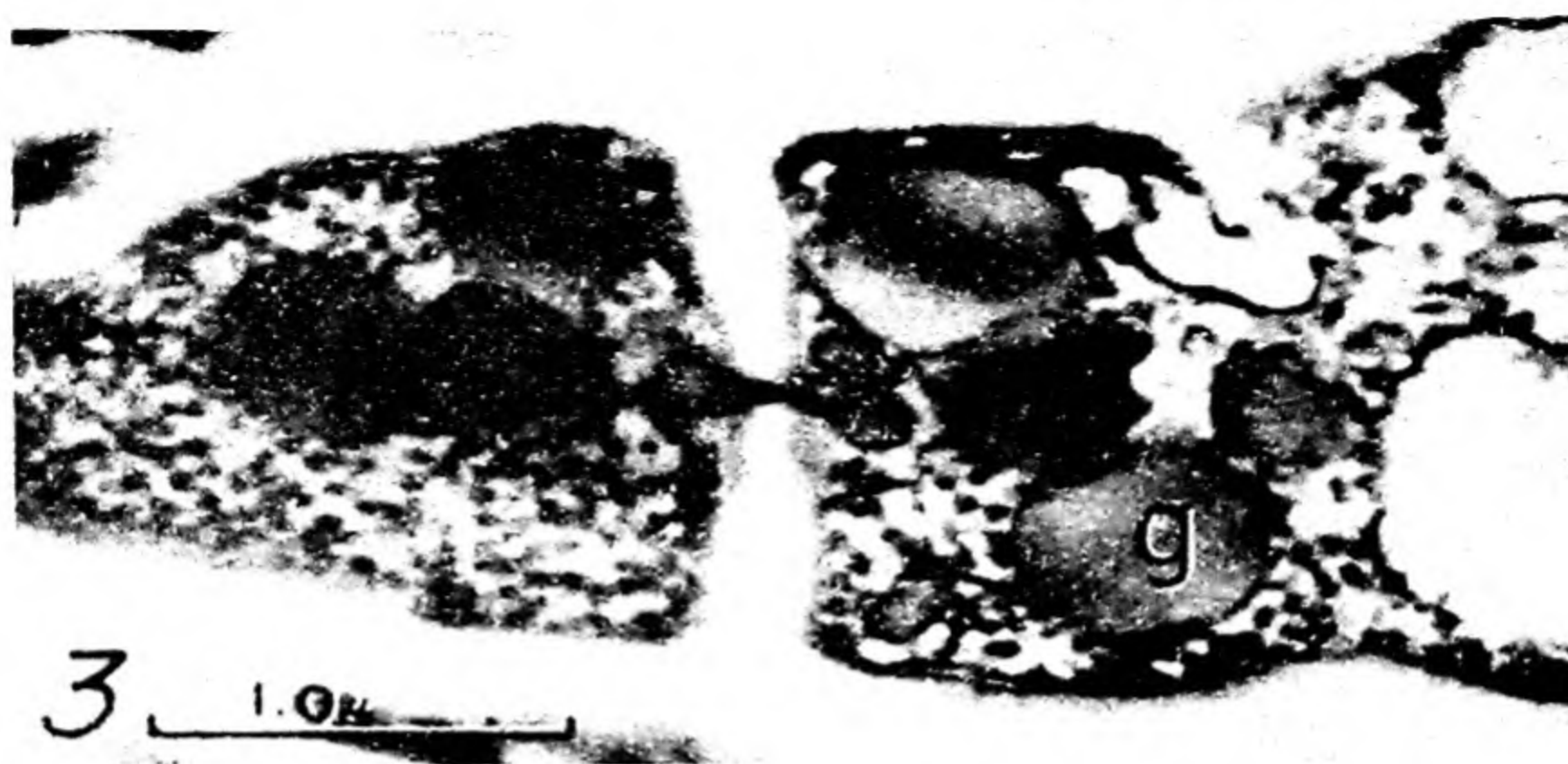


Figure 137. Electron micrograph of a septum in *Aspergillus varicolor*, showing simple perforation. Courtesy Moore and McAlear, 1962, *Am. Jr. Bot.*, 49:86-94.

consists of well-developed, septate, branched hyphae. The compartments or cells are usually multinucleate. The septa are perforated, permitting the streaming of cytoplasm and the migration of nuclei from one cell into the next. The septa of the Deuteromycetes, which might be expected to have ascomycetous affinities, have the same structure as those of the Ascomycetes. Recent electron micrographs (Figure 137) by Moore and McAlear (1962) confirm previous observations with the light microscope.

Growth requirements of a great number of species have been studied. As might be expected, these vary a great deal and there is no point in listing the nutrient requirements of individual species here. If you will consult Lilly and Barnett (1951) and Cochrane (1958), you will find summarized all the information available for particular species. One point of special interest may be mentioned here. There are reports that some Fungi Imperfecti (*Phoma casuarina*, *Phoma* sp.) are able to fix nitrogen, but experimental results are contradictory on this point.

Sporulation. The mycelium of many imperfect fungi, like that of many conidium-producing Ascomycetes, sporulates rather rapidly in culture as well as in nature. In general, species which produce conidia on conidiophores arising directly from the somatic hyphae sporulate more rapidly than those in which conidia are produced in more complex structures, such as pycnidia, sporodochia, or synnemata. The factors which induce or at least favor sporulation have been studied in a number of imperfect fungi, and you will find much

information on this subject in books dealing with the physiology of fungi. The usual factors, temperature, nutrition, pH, light, etc., all affect sporulation. Short exposures to ultra-violet irradiation stimulate conidial production in a number of imperfect fungi (Stevens, 1928). In cultural studies, method of inoculation and amount of media have a profound effect on sporulation (Timnick, Barnett, and Lilly, 1952), and extreme care is needed in performing, recording, and interpreting experiments on this subject. An interesting phenomenon which is often observed in the laboratory is the stimulation of the mycelium of some fungi to sporulate in areas where the hyphae have been cut or injured. I have observed this to be true, particularly with pycnidial fungi. Pycnidia are often produced along a cut surface on the agar sooner and in larger quantities than elsewhere. We have no explanation for this phenomenon. It is possible that hormone-like substances which favor sporulation accumulate along the cut surface and induce formation of sporophores. This is only conjecture, however, and there are other possible explanations.

Sporulation in the Fungi Imperfecti is strictly an asexual process.

Morphology of Reproductive Structures. It is well to review at this time the various methods of conidial production and to say something about the morphology of the structures concerned.

The Conidiophore. Conidia are generally borne on conidiophores which may be produced loosely and indiscriminately by the somatic hyphae or grouped in various types of asexual fruiting bodies. Fungi which produce conidia on more or less loose, cottony hyphae we often term **Hyphomycetes**. Such conidiiferous hyphae may be simple or variously branched. They may be little different from the somatic hyphae and indistinguishable from them, or they may be characteristically marked and provided with sterigmata or specialized branches on which they bear the conidia. Some conidiophores are inflated at the tips, as we have seen in *Aspergillus*; others are inflated at intervals, forming knee-like structures on which the conidia are grouped (*Gonatobotrys*); still others have many branches which are characteristically arranged in whorls (*Verticillium*), in a sympodium (*Monopodium*), or in various other ways (Figure 79). In fact, we can find almost every conceivable variation in the branching or marking of reproductive hyphae among the more than 10,000 species that produce their conidia in this fashion.

A group of conidiophores often unites at the base and part way up toward the tip, and forms a structure we call a synnema (Figure 80D). The top of the synnema is often much branched, the conidia arising at the tips of the numerous branches. In some synnemata the stalk

of the fructification is longer in comparison to the branched top, and the fruiting body resembles a long-handled feather duster. When a large number of conidiophores arise from the surface of a cushion-shaped stroma, the resulting structure is a sporodochium (see page 318).

Considerable attention has been focused on the structure of the conidiophores of the Hyphomycetes, and on the method of conidial production, particularly by Hughes (1953*b*) in Canada and Tubaki (1958) in Japan. Hughes grouped the types of conidiophores and conidial production into eight sections. Tubaki in a later discussion added a ninth section and divided some sections into sub-sections.

The major types of conidial production thus recognized are as follows:

- Section I. Conidia budded off the conidiophores singly or in chains (blastospores).
- Section II. Conidia produced singly from successively formed new growing points; sometimes forming false chains.
- Section III. Thick-walled conidia produced singly from the apex of the conidiophore or its branches, sometimes forming false chains (chlamydospores).
- Section IV. Conidia produced from the apex of a phialide (phialospores).
- Section V. Conidia produced by growth of the apical region of the conidiophore, forming chains which merge imperceptibly with the conidiophore (meristematic arthrospores).
- Section VI. Conidia produced from pores of the conidiophore (porospores).
- Section VII. Conidia produced by fragmentation of the conidiophore (arthrospores).
- Section VIII. Conidia borne singly at apex and laterally on conidiophores which elongate at the base.
- Section IX. Conidia borne singly at apex in such a way as to form false chains with the conidia attached end to side.

As will be noted below, this grouping promises to become the basis for a new classification of the imperfect fungi. Great numbers of developmental studies are now needed to determine how these fungi should be distributed among these sections. Such studies have been in progress for several years and are continuing (see Hughes 1953*b* for references).

The Pycnidium. In a certain group of imperfect fungi, the conidia arise in globose or flask-shaped bodies known as pycnidia. The conidiophores in the pycnidia are generally very short (*Phyllosticta*) (Figure 79A), in some cases almost absent (*Plenodomus*). In the

pycnidia of other fungi, on the contrary, the conidiophores are quite long and distinctly branched (*Dendrophoma*) (Figure 79B). In all cases, they arise from the internal cells of the pycnidial wall. In external appearance, some pycnidia resemble perithecia of some of the Pyrenomycetes, and the only way you can be certain of their nature is to crush them and examine their contents under the microscope. The perithecia, of course, contain asci, whereas the pycnidia contain conidia.

The pycnidial wall is pseudoparenchymatous. Approximately the same variations in configuration can be found in pycnidia as have been described for perithecia. Pycnidia may be completely closed or may have an opening (ostiole); they may be provided with a small papilla or with a long neck leading to the opening; they vary greatly in size, shape, color, and consistency of wall; they may be superficial or sunk in the substratum; they may be uniloculate, simple or labyrinthiform; they may be formed directly by the loose mycelium or may be definitely stromatic. This great variation in pycnidial structure serves to delimit the various form-genera of the pycnidial Deuteromycetes (Figure 138).

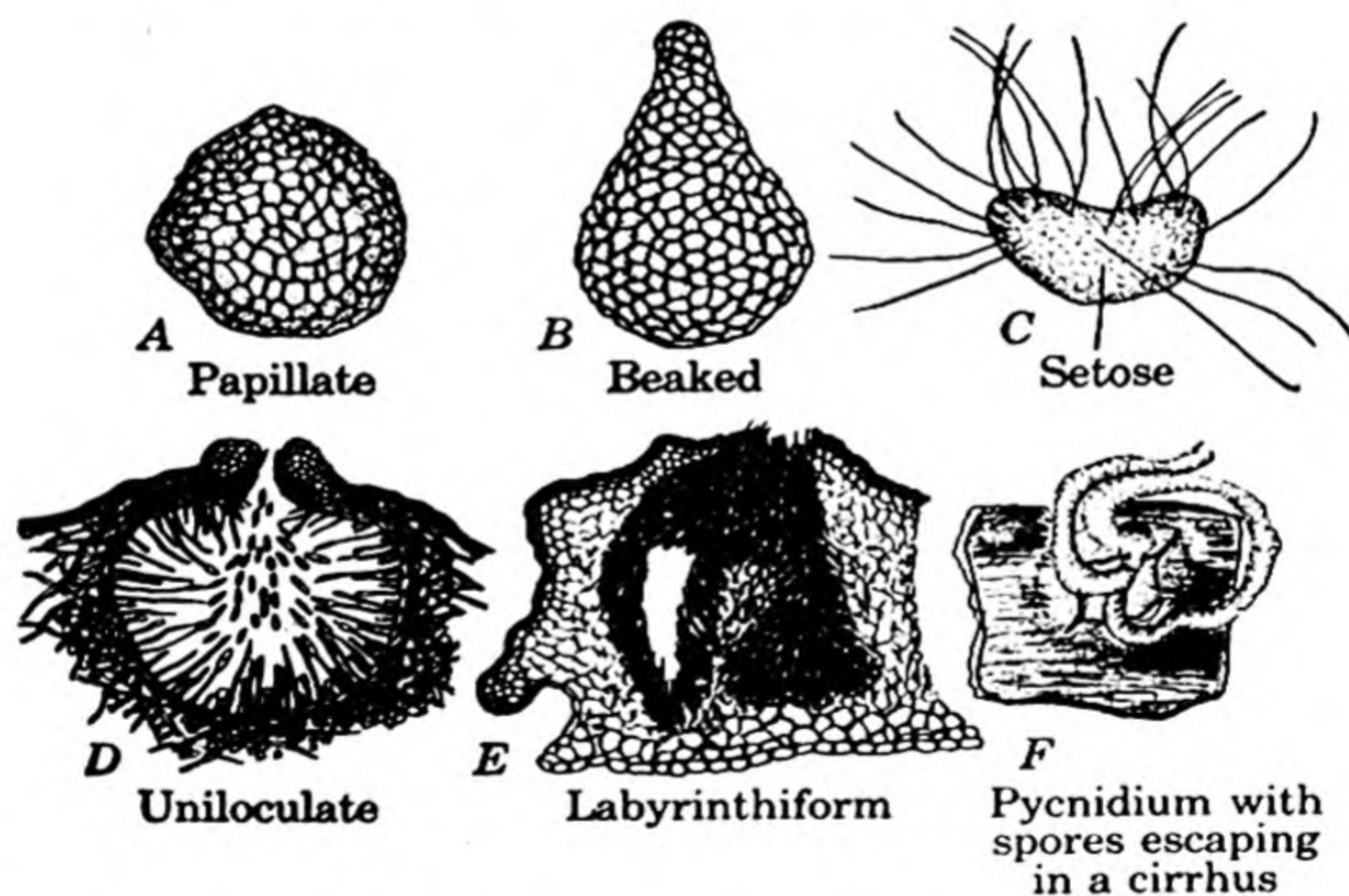


Figure 138. Various types of pycnidia. A. *Zythia fragariae*. B. *Dendrophoma obscurans*. C. *Chaetomella atra*. D. *Diplodia zae*. E. *Fusicoccum viticolum*. F. *Endothia parasitica*, pycnidial stage. C, redrawn from Alexopoulos, 1940, *Mycologia*, 32:336-358; D, redrawn from Burrill and Barrett, 1909, *Ill. Agr. Exp. Sta. Bull.*, 133:63-109; E, redrawn from Reddick, 1909, *Cornell Univ. Agr. Exp. Sta. Bull.*, 263:321-343.

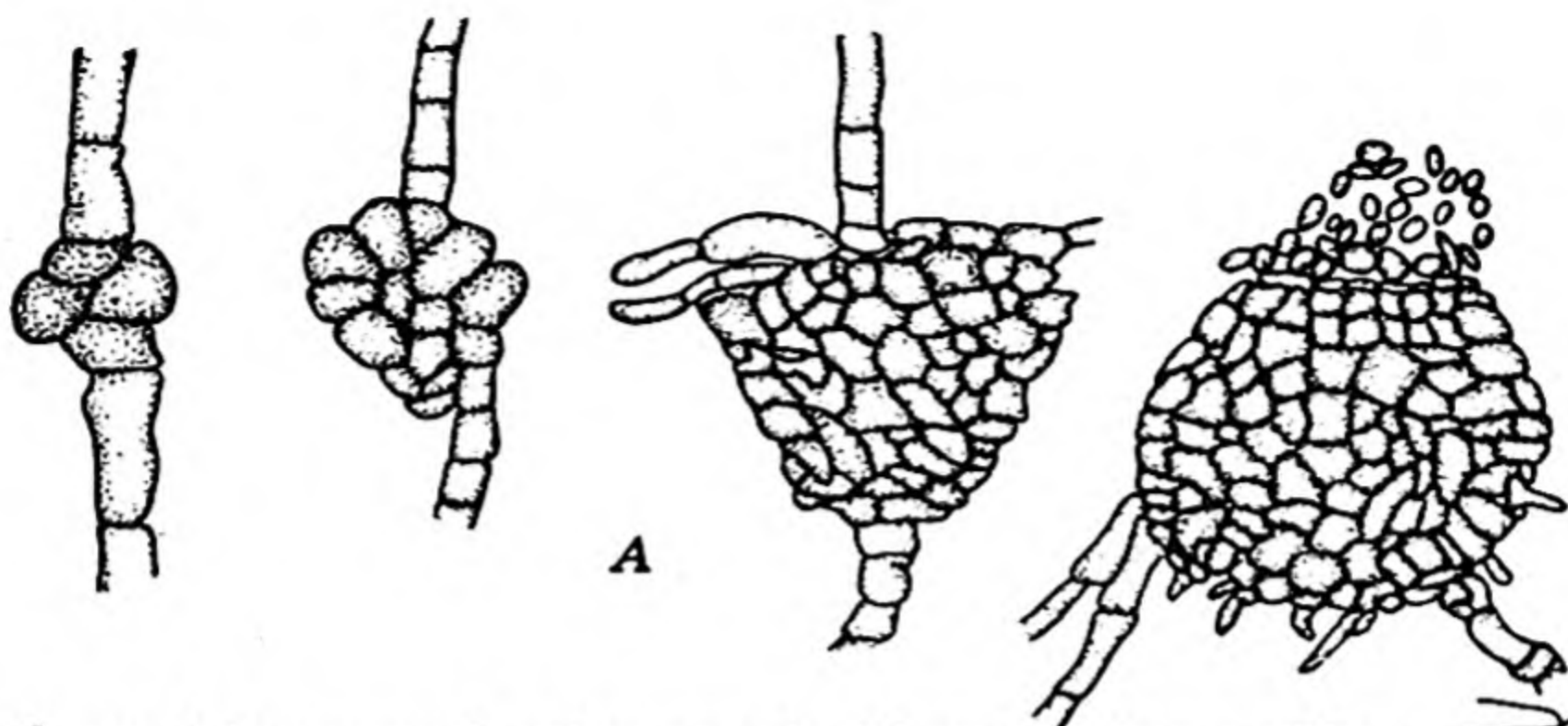
Kempton (1919) found that this group of fungi utilizes three methods of pycnidial production. According to the first, which Kempton calls simple meristogenous, the pycnidium originates from the division of a single cell or a number of adjacent cells in the same hypha (Figure 139A). In the compound meristogenous type, cells of several closely appressed hyphae divide, and later merge to form a pycnidium (Figure 139B). Finally, in the symphogenous type of development, a number of hyphal branches from different hyphae grow toward a common point and interweave to form the pycnidial initial (Figure 139C). From this the pycnidial wall develops, a cavity is formed in the center, and the conidiophores grow out of cells lining the inner wall of the cavity. The conidia, also called pycnidiospores when they are borne in pycnidia, are produced at the tips of the conidiophores.

The Acervulus. The acervulus is typically a flat, open bed of generally short conidiophores growing side by side and arising from a more or less stromatic mass of hyphae. Conidia are borne at the tips of the conidiophores. Some authors do not consider any such structure an acervulus unless it is formed underneath the cuticle or epidermis of a host plant and eventually becomes erumpent. Such a concept, which would define a fungal structure not in terms of its own morphology but rather in terms of its relation to the host, should probably be avoided.

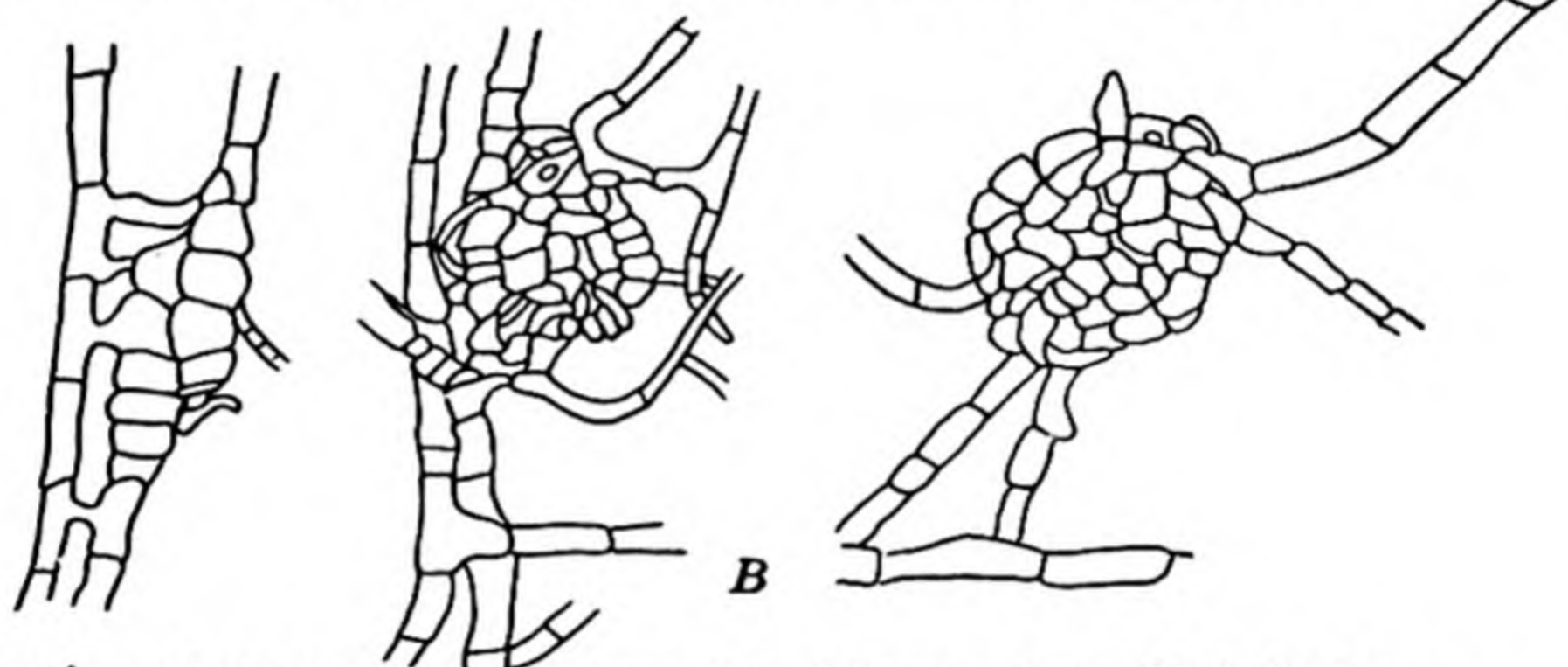
In addition to the conidiophores and interspersed with them, some acervuli produce long, stiff, pointed, dark structures that look like bristles; these are the setae (Figure 141B). Setae may be abundantly formed by certain form-species or may be very sparse. As a matter of fact, it appears that the type of substratum and environmental factors influence this characteristic considerably (Bessey, 1950, pp. 581-582).

The same methods employed for the formation of pycnidia also serve for the formation of acervuli, the origin of which may be simple meristogenous, compound meristogenous, or symphogenous. This undoubtedly explains the fact that intermediate forms between pycnidia and acervuli are produced by some fungi which are, therefore, difficult to classify.

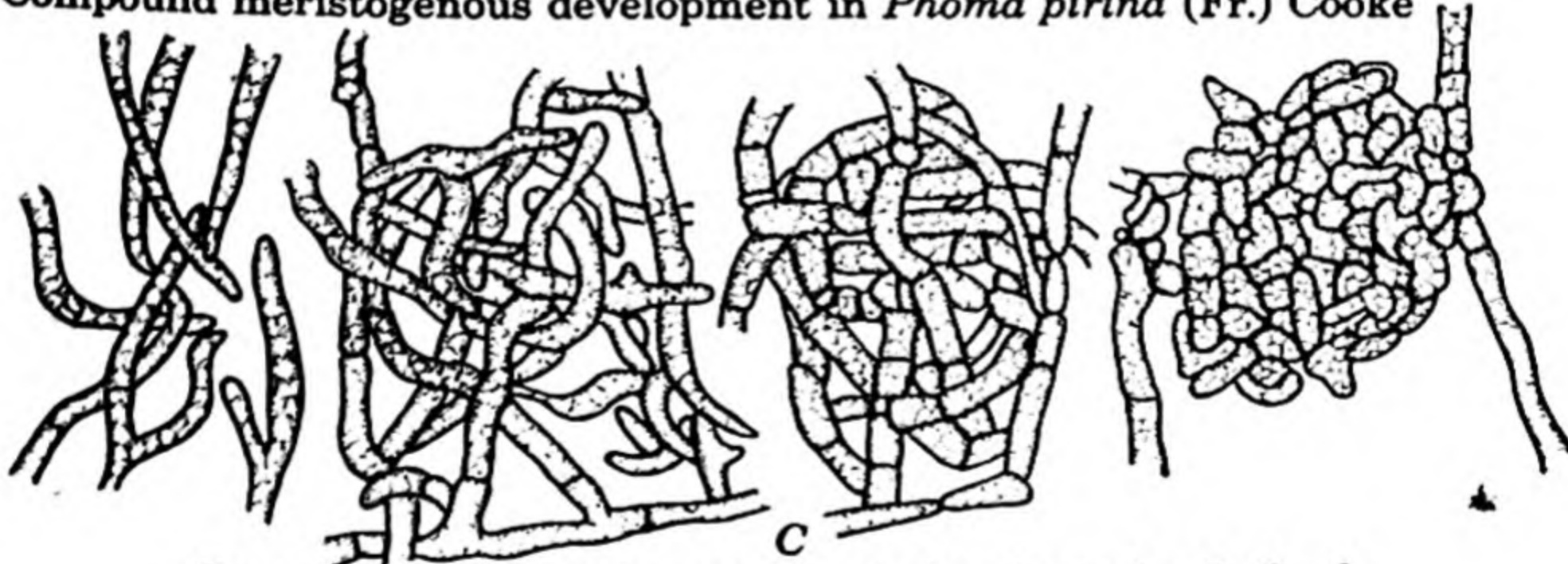
The Spores. Asexually produced spores are usually designated as conidia regardless of their method of origin. As we have already seen, several types of such spores are produced by Ascomycetes and imperfect fungi. In order to distinguish among them many mycologists have adopted a special terminology. We have already defined microconidia (page 225), chlamydospores (page 17), arthrospores



Simple meristogenous development in *Phoma herbarum* West



Compound meristogenous development in *Phoma pirina* (Fr.) Cooke



Symphogenous development in *Zythia fragariae* Laibach

Figure 139. Three types of pycnidial development. A, B, redrawn from Kempton, 1919, *Bot. Gaz.*, 68:233-261, by permission of University of Chicago Press, Chicago; C, redrawn from Miss Huang, 1949, M.S. Thesis, Michigan State College.

(page 17), and blastospores (page 221). **Phialospores** (Gr. *phialis* = phial) are formed in succession from a special bottle-shaped structure (phialid). They often adhere in long chains, or may become detached and adhere in irregular groups. **Porospores** (Gr. *poros* = pore) are spores which are produced from pores of a conidiophore. Conidia formed in pycnidia are usually called pycnidiospores.

Conidia are also named in accordance with their shape or structure. Thus we have **dictyospores** (Gr. *dictyon* = net), which possess both vertical and horizontal septa; **scoleospores** (Gr. *skolex* = worm), which are greatly elongated or worm-like; and **heliospores** (Gr. *helix* = helix), which are coiled. These latter terms describing the shape of spores are used for any type of spore which exhibits that shape regardless of its origin or its nature. Thus, the ascospores of *Myriangium bambusae* (Figure 131) and those of *Pleospora* are dictyospores. So are the conidia of *Alternaria* (Figure 144H).

The Parasexual Cycle. If you refer to our general discussion of the fungi in Chapter 1, you will find that the parasexual cycle was defined as a cycle in which plasmogamy, karyogamy, and haploidization take place, but not at a specified time or at specified points in the life cycle of an organism. We shall now discuss in a little more detail this mechanism, of particular importance to the imperfect fungi, in which no true sexual cycle occurs.

Parasexuality was first discovered in 1952 by Pontecorvo and Roper of the University of Glasgow in *Aspergillus nidulans*, the imperfect stage of *Emmericella nidulans*. Since then parasexual phenomena have been identified in several imperfect fungi which possess no sexual stage, as well as in Basidiomycetes and in Ascomycetes other than *Emmericella nidulans*. The following discussion is based chiefly on that of Professor G. Pontecorvo (1956, 1958).

The sequence of events in a complete parasexual cycle is somewhat as follows:

1. Formation of heterokaryotic mycelium.
2. Fusion between two nuclei.
 - a. Fusion between like nuclei.
 - b. Fusion between unlike nuclei.
3. Multiplication of diploid nuclei side by side with the haploid nuclei.
4. Occasional mitotic crossing-over during the multiplication of the diploid nuclei.

5. Sorting out of diploid nuclei.
6. Occasional haploidization of the diploid nuclei.
7. Sorting out of new haploid strains.

Let us discuss each step briefly and point out its consequences on the genetic make-up of these fungi.

Formation of Heterokaryotic Mycelium. There are several ways in which a heterokaryotic mycelium may be formed. The most common way perhaps is by the anastomosis of somatic hyphae of different genetic constitutions. The foreign nucleus or nuclei introduced into a mycelium multiplies and its progeny spread through the mycelium, rendering the latter heterokaryotic. Another way in which a homokaryotic mycelium may change into heterokaryotic is by mutation in one or more nuclei, as has been shown to occur in some Ascomycetes (Wilson and Alexopoulos, 1956). Still a third way is by the fusion of some of the nuclei and their subsequent multiplication and spread among the haploid nuclei. This would result in a mixture of haploid and diploid nuclei and therefore, etymologically at least, in a heterokaryotic mycelium. However, since no new genetic combination would be formed, this type of heterokaryosis is probably not very significant.

Karyogamy and Multiplication of Diploid Nuclei. That nuclei fuse in a mycelium has been adequately demonstrated. When a mycelium has become heterokaryotic, nuclear fusion takes place between haploid nuclei of different genotypes as well as between nuclei of the same type. The former results in a heterozygous diploid nucleus; the latter, in a homozygous diploid nucleus. Thus at this stage the mycelium may contain at least five types of nuclei: two types of haploid, two types of homozygous diploid, and heterozygous diploid nuclei. All these nuclei presumably multiply at about the same rate, but the diploid nuclei are present in much smaller numbers than the haploid. Pontecorvo (1958) estimates a proportion of 1 diploid heterozygous nucleus to 1000 haploid nuclei.

Mitotic Crossing-over. During multiplication of the diploid nuclei, mitotic crossing-over occasionally takes place. This results in new combinations and new linkages and is probably the most important phase of the parasexual cycle. These recombinations, which are dependent on the existence of heterokaryosis, give the fungus some of the advantages of sexuality within the parasexual cycle. Pontecorvo calculates that the amount of recombination which may be expected to occur in an ascomycete through its parasexual mechanism is 500 times smaller than through its sexual mechanism. It is

significant, however, that in *Penicillium chrysogenum* and *Aspergillus niger*, neither of which is known to reproduce sexually, diploidization and mitotic crossing-over occur much more frequently, so that the importance of the parasexual cycle in the Fungi Imperfecti may be as great as that of the sexual cycle in other fungi, from the standpoint of the evolution of the species.

Sorting Out of Diploid Strains. In fungi which produce uninucleate conidia, sorting out of the diploid nuclei occurs by their incorporation into conidia which then germinate and produce diploid mycelia. Diploid strains of several imperfect fungi have been isolated. The first such instance was recorded in 1952 by J. A. Roper, who synthesized and isolated diploid strains of *Aspergillus nidulans*. As might be expected, the conidia of diploid strains were somewhat larger (1.3 times) than those of the haploid parents.

Haploidization. Diploid colonies will often produce sectors which may be recognized by various methods (see Pontecorvo, 1958). These sectors produce haploid conidia which may be isolated and grown into haploid colonies. This means that some diploid nuclei undergo haploidization in the mycelium and are sorted out. Some of these haploid strains are genotypically different from either parent because of mitotic recombinations producing new linkage groups, which are sorted out in the haploid conidia.

What is the nuclear situation then in a mycelium which has become heterokaryotic by the introduction of foreign nuclei through hyphal fusion with another strain? After the parasexual cycle has operated for some time, such mycelium may contain haploid nuclei like those of both parents, haploid nuclei with various new genetic recombinations, homozygous diploid nuclei of various types, and heterozygous diploid nuclei of various types. How frequently does this situation occur in nature? Heterokaryosis is of common occurrence, as evidenced by the various strains of almost any species that may be isolated at random from natural substrata. Wild diploid strains do not appear to be common, but have been found (Jinks, 1952b).

Classification. Since thousands of imperfect fungi do not fit our classification system, because it is based on the characters of the sexual stage, a practical need has arisen for a convenient system, artificial though it be, the chief purpose of which is to provide a method of identifying and naming these organisms. Accordingly, we group all these fungi into the form-class Deuteromycetes, which we subdivide into a number of form-orders, form-families, form-genera, and form-species. In each of these categories we group

fungi which have in common some morphological characteristics of their conidial stages, and which we can, therefore, conveniently identify and catalog. By such groupings, however, in no way do we imply that the organisms we place in any one group are related, for we cannot surmise relationships in fungi unless we know the sexual stages. *Two fungi whose conidial stages are almost exactly alike, and which, therefore, we would classify in the same form-genus, might have sexual stages which are sufficiently different to place them in different ascomycetous genera.* For example, *Septoria rubi* and *Septoria avenae*, two "imperfect fungi" which we had classified in the form-genus *Septoria* on the basis of their conidial stages, were found to have perfect stages, one of which belongs to the ascomycetous genus *Mycosphaerella* (*Mycosphaerella rubi*), and the other to the ascomycetous genus *Leptosphaeria* (*Leptosphaeria avenaria*).

Similarly, *two Ascomycetes belonging to the same ascomycetous genus may have vastly different conidial stages.* For example, *Mycosphaerella fragariae* on strawberry forms its conidia at the tips of long, loosely produced, unorganized conidiophores, whereas the aforementioned *Mycosphaerella rubi* on raspberry bears its conidia on very short conidiophores inside a pycnidium. In accordance with our artificial system of classification of the Deuteromycetes, we would place the conidia of *Mycosphaerella fragariae* in the form-genus *Ramularia*, which belongs in the form-order Moniliales, but those of *Mycosphaerella rubi* in the form-genus *Septoria*, which belongs to the form-order Sphaeropsidales. Once you understand this situation you will have no difficulty in grasping and accepting the seemingly complicated and confused state of affairs arising from the existence of this large group of fungi.

The convenience of such a system of classification for the imperfect fungi has been carried further to include the conidial stages of known Ascomycetes. Since many Ascomycetes, particularly the parasitic ones, form their ascocarps but once a year, we are much more likely to encounter these fungi in their conidial stages. By including these stages in the general scheme of classification of the Deuteromycetes, we can identify a fungus by its conidial stage without having to wait for it to develop its ascus stage. This, of course, results in two names for each ascomycete whose conidial stage was discovered before its perfect stage: one name—the valid one—which we give to the ascigerous stage to indicate its relationships, and one name—a synonym—which indicates the type of conidia the fungus produces. For example, we have seen in Chapter 17 that *Venturia*

inaequalis, the cause of apple scab, produces one- or two-celled, brown conidia on short conidiophores which are closely ringed. As these are the characters of the form-genus *Spilocaea*, we often refer to the imperfect stage of *Venturia inaequalis* as *Spilocaea pomi*, the name given to the fungus before the perfect stage was discovered. Since, according to the International Rules of Botanical Nomenclature, a member of the Plant Kingdom may have but one valid name, *Venturia inaequalis* is the valid name of the fungus. But, since the name *Spilocaea* indicates the precise type of conidial stage produced, mycologists find it more convenient to say that *Venturia inaequalis* has a *Spilocaea* imperfect stage than to describe the conidia and conidiophores in many words. For this reason we often write the name of the imperfect stage of an ascomycete in parentheses after the valid name thus: *Venturia inaequalis* (= *Spilocaea pomi*); or still more properly: *Venturia inaequalis* (Cke.) Wint. [= *Spilocaea pomi* Fr. ex Fr.]. The naming of the conidial stages is so convenient and has been adopted so widely that the International Botanical Congress decided at its Stockholm meeting in 1950 to legalize the use of form-names for conidial stages, still recognizing, of course, the name of the perfect stage as the official name for the entire organism. Thus, when we speak or write about the apple scab fungus *as a whole*, or of its ascus stage in particular, we use the name *Venturia inaequalis*, but when we are dealing with the conidial stage of this fungus it is convenient—and now legal and proper—to refer to it as *Spilocaea pomi*.

Characteristics Used in Classification. The characteristics we use for the classification of the Deuteromycetes are the type of fructification and the shape, color, and septation of the conidia. Types of fructification form the basis for separation of form-orders. We place those fungi which produce their conidia in pycnidia in the form-order Sphaeropsidales; all those which form acervuli, in the Melanconiales; and those which reproduce in any other way (budding, fragmentation of hyphae into oidia, loose conidiophores, sporodochia, or synnemata), in the Moniliales. A group of fungi also exists in which no conidia or other reproductive cells are known. These we place in the form-order Mycelia Sterilia. Many of the Mycelia Sterilia, when their perfect stages were discovered, proved to be Basidiomycetes.

The Sphaeropsidales and Moniliales are subdivided into a number of form-families, the first on the basis of pycnidial characters such as shape, color, and consistency of wall, the second on the basis of conidiophore grouping and color. The Melanconiales comprise only one form-family, the Melanconiaceae. The Mycelia Sterilia are an as-

semblage of form-genera so heterogeneous that we make no attempt whatever to organize them into form-families.

Form-genera of the Deuteromycetes are based on such characters as type of conidiophores and color, shape, and septation of conidia. Form-species are based almost entirely upon the host on which they are found and the size of their conidia.

The Saccardian System. Because of the great number of form-genera in the Deuteromycetes (Bender listed 1335 in 1931), Saccardo (1899) proposed a breakdown of the classification into groupings (sections) of form-genera in accordance with conidial characters. This is a very convenient system which mycologists the world over have adopted.

The "section" is not an official category in the classification system, but rather a convenient group of form-genera under each form-family, which exhibit the same conidial characters as far as shape, color, and septation are concerned.

The sections proposed by Saccardo (1899) are the following:

Amerosporae: Conidia continuous, spherical, ovoid to elongated, or short cylindric.

Allantosporae: Conidia cylindric, curved (allantoid), hyaline to pale.

Hyalosporae: Conidia hyaline.

Phaeosporae: Conidia colored.

Didymosporae: Conidia ovoid to oblong, one-septate.

Hyalodidymae: Conidia hyaline.

Phaeodidymae: Conidia colored.

Phragmosporae: Conidia oblong, two- to many-septate (transversely septate).

Hyalophragmiae: Conidia hyaline.

Phaeophragmiae: Conidia colored.

Dictyosporae: Conidia ovoid to oblong; net-septate (transversely and longitudinally septate).

Hyalodictyae: Conidia hyaline.

Phaeodictyae: Conidia colored.

Scolecosporae: Conidia thread-like to worm-like; continuous or septate, hyaline or pale.

Helicosporae: Conidia spirally cylindrical; continuous or septate; hyaline or colored.

Staurosporae: Conidia stellate (star-shaped), radially lobed; continuous or septate; hyaline or colored.

Validity of Taxonomic Characters. The first criterion in judging the validity of a taxonomic character is its stability under a variety of environmental conditions. Obviously, a characteristic which changes "with the wind" is not a good one to use in separating taxonomic

categories. In order to discover, however, the stability of a certain characteristic, much experimental work is required which not only is time-consuming but also requires elaborate equipment for the control of the environment. A considerable amount of experimental work has shown that many of the characteristics used in delimiting form-genera of the Deuteromycetes are quite unstable under different environmental conditions, at least in artificial culture. Taxonomists have criticized such experiments because the fungus is subjected to conditions so unnatural—synthetic culture media—that its behavior cannot be said to represent what actually occurs in nature. Much more valid would be results obtained by a study of the behavior of the fungus on its natural substratum subjected to a variation of such factors as temperature, moisture, humidity, and light at the time the fungus is about to fruit. Reports of such experiments are much less frequent in the literature, but those that do exist throw considerable doubt on the validity of certain characteristics used in delimiting form-genera and species.

The custom of naming species of Deuteromycetes purely on the basis of the host on which they are found is admittedly unscientific and has resulted in the naming of hundreds of non-existent "species." This procedure is chiefly responsible for the recording of over 1000 species for such form-genera as *Septoria*. These species are differentiated chiefly on the basis of host. Cross-inoculations of different hosts would probably show that a great many of these so-called species represent one and the same fungus. This situation is well presented by N. A. Cobb, whom Stevens (1913) quoted as follows: "Is a fungus species newly found on a peach? Call it new and name it *pruni*. Same genus on the grape—name it *ampelina*. On the apple? New, call it *mali*. On banana? Christen it *musae*. What next? Sparrow on a pear tree, *Passer pyri*?"¹

This chaotic condition, in which the classification of the Deuteromycetes has been allowed to remain these many years, has not disturbed some taxonomists. They have felt that the Deuteromycetes were not worth considering because there appeared to be no hope of ever arranging them in a phylogenetic system. However, inasmuch as a great many Deuteromycetes probably possess no sexual stage and are evolving as conidial fungi, it is not impossible that phylogenetic relationships may become evident if we were to use a different basis for classification.

We have seen that Hughes (1953b) and Tubaki (1958) are at-

¹ Quoted by permission of The Macmillan Co., New York.

tempting to classify the Hyphomycetes on the basis of conidiophore structure and conidial development. This seems to be a much more natural foundation for a classification system, and it is probable that it will eventually replace the Saccardian system when all the known form-genera have been studied and their probable affinities have been determined. In the meantime the search for perfect stages should continue, and Professor Tubaki's serious attempts (1958) to discover a pattern of relationships between perfect and imperfect stages should certainly be expanded.

To discover the genus to which an imperfect fungus belongs, Barnett's *Illustrated Genera of Imperfect Fungi* (1960) is very helpful.

KEY TO THE FORM-ORDERS OF THE DEUTEROMYCETES

- | | |
|---|-------------------------|
| A. Reproduction by means of conidia, by oidia, or by budding | |
| B. Reproduction by means of conidia borne in pycnidia | <i>Sphaeropsidales</i> |
| BB. Conidia, when formed, not in pycnidia | |
| C. Reproduction by means of conidia borne in acervuli | <i>Melanconiales</i> |
| CC. Reproduction by means of conidia borne otherwise, by oidia, or by budding | <i>Moniliales</i> |
| AA. No reproductive structures known | <i>Mycelia Sterilia</i> |

form-order SPHAEROPSIDALES

We subdivide the Sphaeropsidales into four form-families which we distinguish as follows: Sphaeropsidaceae—pycnidia dark colored, leathery to carbonous, stromatic or non-stromatic, generally (but not always) provided with a circular opening; Zythiaceae—pycnidia as in the Sphaeropsidaceae, but light colored instead of dark, and soft or waxy instead of leathery; Leptostromataceae—pycnidia shield-shaped or elongate, flattened; Excipulaceae—mature pycnidia more or less deeply cup-shaped.

form-family SPHAEROPSIDACEAE

According to Bender, this form-family contained 568 form-genera in 1931. More have been described since that time. Most of the species included are saprobes, but a good number are parasitic, causing serious diseases of plants. Among the most common of the

Hyalosporae are the form-genera *Phyllosticta*, *Phoma*, *Macrophoma*, *Dendrophoma*, and *Phomopsis*. As most mycologists define the first two of these, there is no real distinction between them, and it has been advocated that they be united under the older name *Phoma*. (See Grove, 1935, for a discussion of this question.) The distinction between them and *Macrophoma* is purely artificial. As they stand today, all three genera are characterized by small, ostiolate pycnidia sunk in the substratum, very short conidiophores, and hyaline, spherical or oval spores. If the fungus grows on leaves, it is placed in the form-genus *Phyllosticta*; if on stems, it is *Phoma* or *Macrophoma*, depending on whether the conidia measure up to 15 μ (*Phoma*) or over 15 μ (*Macrophoma*). Thus, if one and the same fungus parasitizes both the leaves and stems of a plant (a common occurrence) and its conidia measure 10–20 μ (not an excessively large range), it exhibits characteristics of all three of these form-genera! Obviously, this is neither logical nor convenient. *Dendrophoma* is distinguished from the preceding form-genera by its long, branched conidiophores. *Phomopsis* produces two types of pycnidiospores (Figure 140C). One type is indistinguishable from those of *Phoma*; the other type, called **stylospores** (Gr. *stylos* = pillar + *sporos* = spore), is elongated and, in some species, bent at the top like a walking stick. Stylospores have never been seen to germinate and their function is unknown. There appears to be a definite genetic connection between the form-genus *Phomopsis* and the ascomycete genus *Diaporthe* (Pyrenomycetes, Diaporthales, Diaporthaceae). All perfect stages found up to now to be connected with *Phomopsis* imperfect stages have proved to belong to the genus *Diaporthe*.

Phyllosticta acericola, which causes a serious leaf spot of maple, *Phyllosticta solitaria*, the cause of apple blotch, *Phoma oleracea*, which seriously attacks cabbage, *Dendrophoma obscurans* (Figures 79B, 138B, 140B), the cause of strawberry leaf blight, and *Phomopsis pseudotsugae*, which causes a die-back of various conifers in Europe (Butler and Jones, 1949), are but a few of the more economically important form-species in the Hyalosporae.

Among the Phaeosporae, the form-genera *Sphaeropsis* and *Coniothyrium* are the most common. Both have dark conidia, differing only in size. In *Sphaeropsis* the conidia are large; in *Coniothyrium* they are small (Figures 140D, E). *Sphaeropsis malorum* (the imperfect stage of *Physalospora cydoniae*), which is parasitic on apple, causes black rot of the fruit and frog-eye spot of the leaves. *Conio-*

thyrium diplodiella (the imperfect stage of *Leptosphaeria coniothyrium*) parasitizes raspberry canes.

Ascochyta (Figure 140G) has two-celled hyaline conidia, and *Diplodia* (Figures 138D, 140H) has two-celled brown conidia. *Diplodia natalensis* is a destructive parasite of citrus and a number

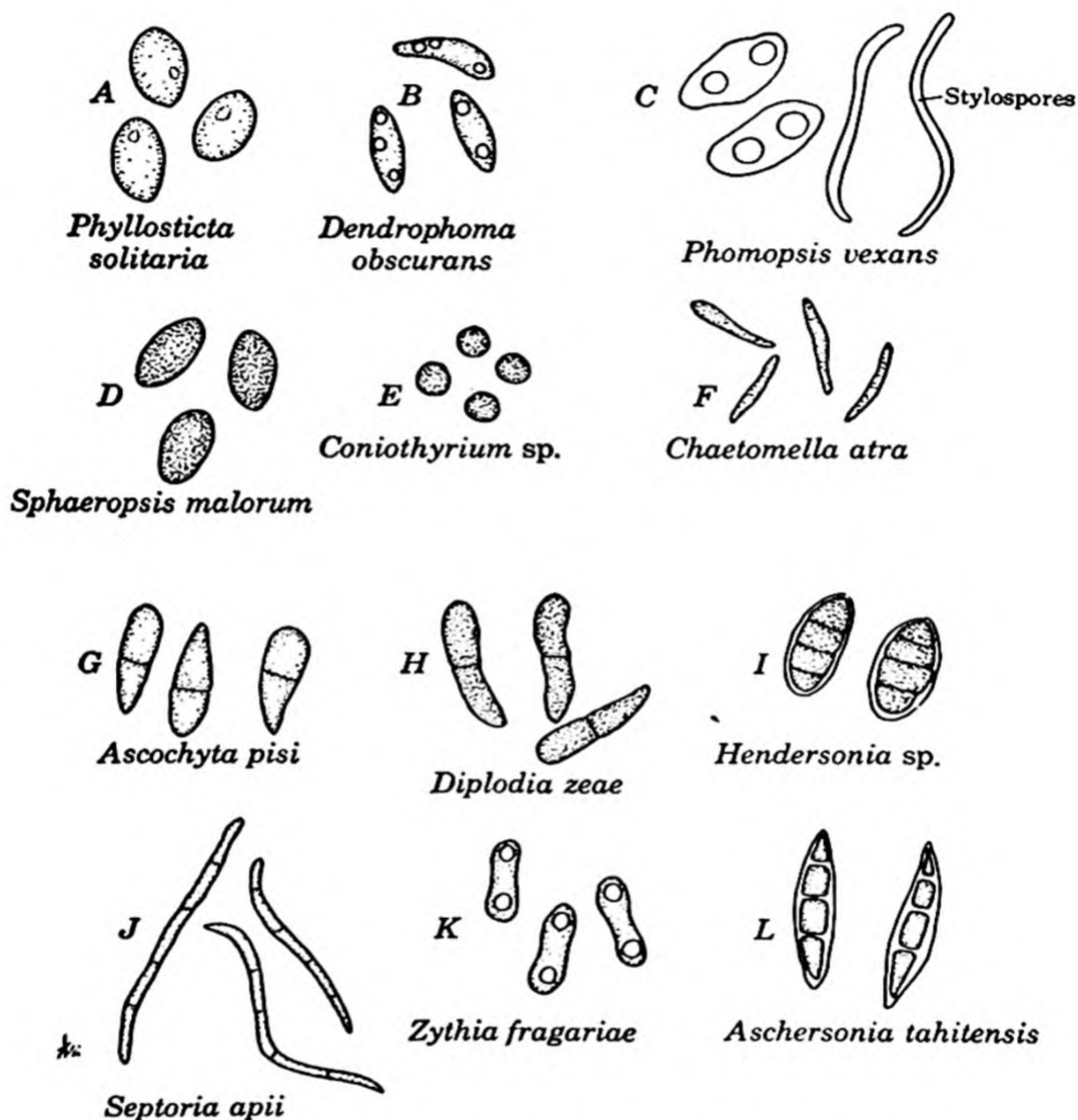


Figure 140. Various types of pycnidiospores of the Sphaeropsidales. C, redrawn from Butler, 1948, M.S. Thesis, Michigan State College; F, redrawn from Alexopoulos, 1940, *Mycologia*, 32:336-358; L, redrawn from Montagne, in Engler and Prantl, 1900, *Die natürlichen Pflanzenfamilien*, Teil I, Abt. 1^{oo}, Wilhelm Engelmann, Leipzig.

of other cultivated crops in the tropics and subtropics. *Hendersonia* (Figure 140I) has many-celled, brown conidia.

One of the most common and widespread form-genera of the Sphaeropsidaceae is *Septoria* of the section *Scolecosporae*. The pycnidium of *Septoria* is much like that of *Phoma*, but the conidia are long and slender, with one or more septa (though sometimes aseptate), generally curved and always hyaline or greenish. *Septoria apii* (Figures 80A, 140J), the cause of late blight of celery, *Septoria chrysanthemella*, the cause of leaf spot of *Chrysanthemum*, and *Septoria lycopersici*, the cause of leaf spot of tomato, are three destructive parasites in this ubiquitous form-genus. Several well-known Ascomycetes have *Septoria* imperfect stages. Two of the most common are *Mycosphaerella sentina* (= *Septoria pyricola*), the cause of pear leaf spot, and *Mycosphaerella rubi* (= *Septoria rubi*), the cause of leaf spot of raspberries.

form-family ZYTHIACEAE

This is a fairly large family which, however, contains few economically important species. The pycnidia are generally light or brightly colored, and their walls are soft or waxy. They may be either stromatic or non-stromatic. *Aschersonia* (Figure 140L), a common form-genus of insect parasites, has been employed in the biological control of scale insects in Florida and elsewhere where the climate is humid enough to favor the spread of the fungi in epizoötic proportions (Gr. *epi* = upon + *zoön* = animal; equivalent to epidemic, but applied to animals). *Zythia* is another genus which forms pycnidia characteristic of this family. *Zythia fragariae* (the imperfect stage of *Gnomonia fragariae*) (Figures 138A, 140K) is the cause of strawberry leaf blotch in England, and is associated with stem-end rot of strawberries in France, in Michigan, and in Canada.¹

form-order MELANCONIALES

All the Melanconiales are assembled into a single form-family, the Melanconiaceae. Many are parasitic on plants and cause a group of diseases called anthracnoses. The acervuli, which are the characteristic structures of this form-family, generally develop below the cuticle or below the epidermis of the host. Becoming erumpent when

¹ *Gnomonia fructicola*, described from Canada, is probably the same fungus.

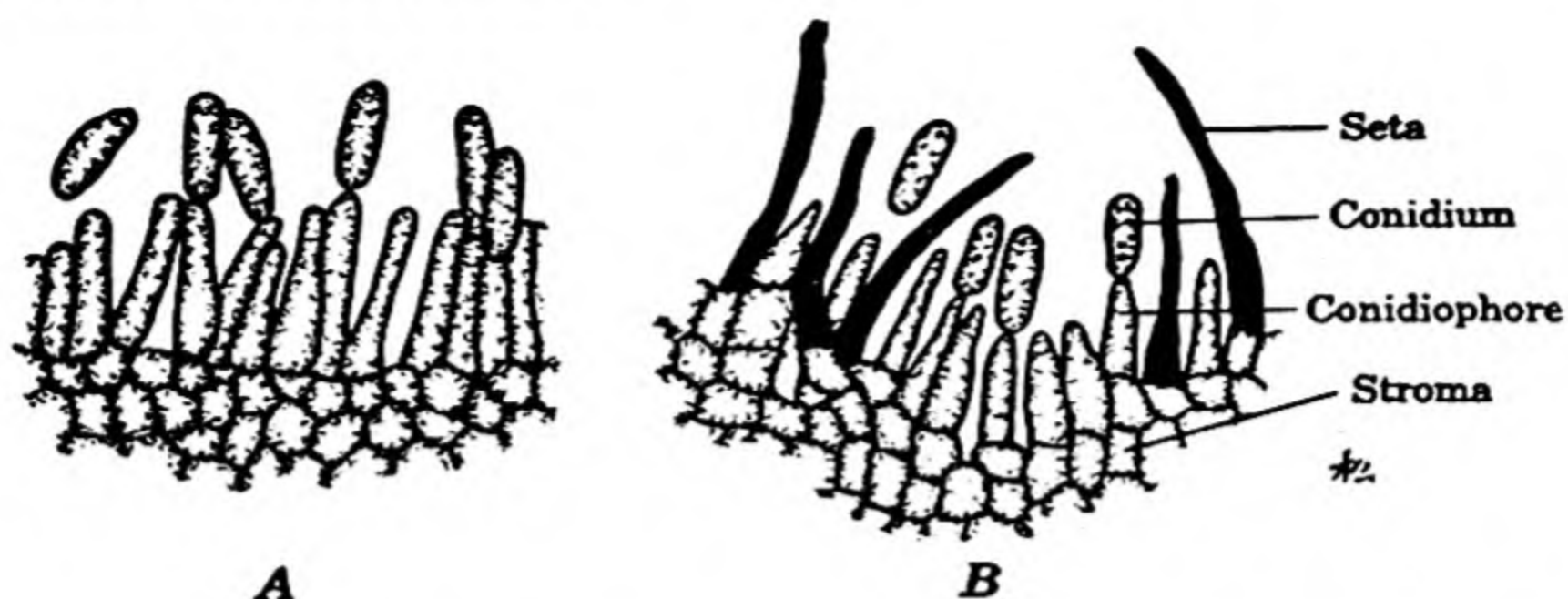


Figure 141. Acervuli. A. *Gloeosporium* sp. B. *Colletotrichum lindemuthianum*.

the conidia are mature, they release them in characteristic droplets which may be white, cream, pink, orange, black, or other color, depending on the pigmentation of the conidia.

In the Hyalosporae, *Gloeosporium* and *Colletotrichum* are the two most common genera. Their conidia are typically elongated with rounded ends and, characteristically, are slightly narrower in the middle than at the ends. The only difference between the two form-genera is that *Colletotrichum* produces dark brown, long setae in the acervulus, whereas *Gloeosporium* does not (Figure 141). As mentioned on page 315, however, this characteristic is so variable that its validity in separating two form-genera is questionable.

Gloeosporium musarum (*Colletotrichum musae*, according to von Arx, 1957) (Figure 142B) is perhaps the most important form-species of *Gloeosporium* whose perfect stage has not been found. *Colletotrichum lagenarium*, the cause of watermelon anthracnose,¹ and *Colletotrichum atramentarium*, the cause of black-dot root rot of tomato and eggplant, are probably the only form-species in this form-genus which cause serious trouble. But a number of Ascomycetes, which are well-known plant pathogens, have *Colletotrichum* imperfect stages. Among the latter is *Glomerella cingulata* (Pyrenomyces, Diaporthales, Diaporthaceae), which attacks a great number of host plants, causing anthracnose. By means of cultural experiments Shear and Wood (1907) demonstrated that isolates of the fungus from all these hosts are indistinguishable morphologically and that setae may be present in some acervuli and absent in others in

¹ *Glomerella lagenaria* was reported in 1931 as the perfect stage of this fungus, produced in culture by ultra-violet irradiation of the mycelium. Inasmuch as mature ascocarps were never seen, this report must await confirmation before it can be accepted.

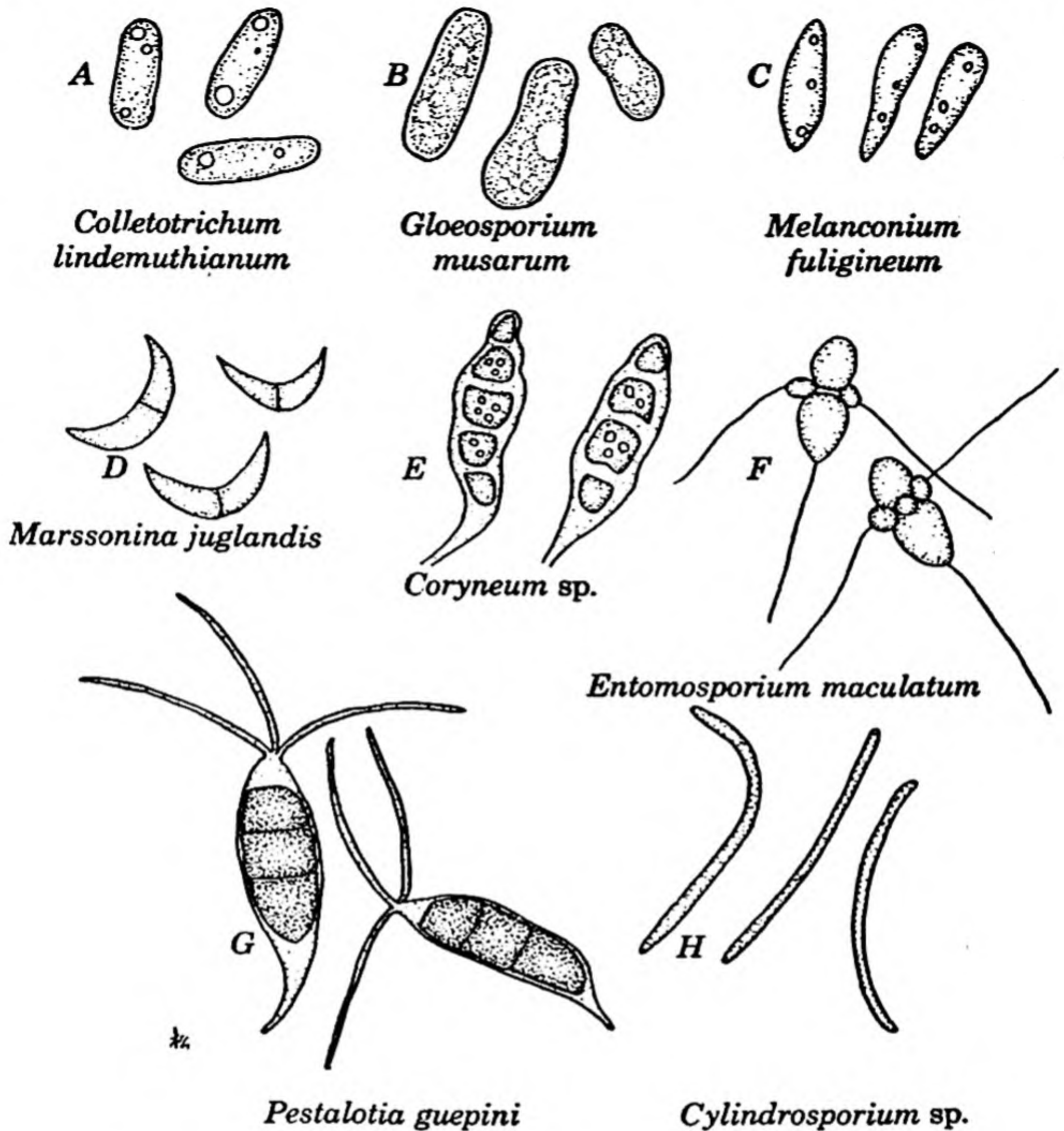


Figure 142. Various types of conidia of the Melanconiales.

the same isolate. This gives us the perfect reason for combining the two form-genera *Gloeosporium* and *Colletotrichum*, since the same fungus exhibits characteristics of both. *Glomerella lindemuthiana* (= *Colletotrichum lindemuthianum*) (Figure 142A), the cause of the very serious and common bean anthracnose, is another fungus in this group.

Melanconium fuligineum, the cause of bitter rot of grapes, belongs to the section *Phaeosporae* (Figure 142C). The physiology of its sporulation has been studied in culture (Timnick and coworkers

1951, 1952). In the Hyalodidymae, *Marssonina populi* is the cause of leaf and twig blight of poplar. *Marssonina juglandis* (Figure 142D) (the imperfect stage of *Gnomonia leptostyla*) causes anthracnose of walnut and related hosts. *Marssonina rosae* (the conidial stage of *Diplocarpon rosae*) causes the very serious and widespread black spot of roses. *Marssonina fragariae* (the conidial stage of *Diplocarpon earliana*) causes strawberry leaf scorch. The conidia of *Marssonina* are two-celled and hyaline. *Coryneum beyerinckii*, with many-celled, dark conidia (Phaeophragmiae), is a very common parasite of stone fruits in this country and in Europe, causing *Coryneum* canker of peaches, apricots, and almonds. *Entomospodium maculatum* (Figure 142F) (the imperfect stage of *Diplocarpon soraueri*) has many-celled conidia. Each is provided with hyaline setae and resembles an insect, hence the name *Entomospodium*. This form-genus produces its conidiophores in a structure intermediate between a pycnidium and an acervulus. Some authors, regarding this structure as an acervulus, place this form-genus in the Melanconiaceae, but others classify it in the Leptostromataceae of the Sphaeropsidales. The form-genus *Pestalotia*, including its segregant *Monochaetia*, contains 286 form-species (Guba, 1961) many of which are parasitic. *Pestalotia guepini* (Figure 142G) attacks camellias and other ornamentals. It also causes a serious anthracnose of the tea plant.

The form-genus *Cylindrosporium* (Figure 142H) is the most important one of the Scolecosporae. The universally common *Higginsia hiemalis* (Discomycetes, Helotiales), which causes leaf spot of cherries, has *Cylindrosporium hiemale* as its imperfect stage. Several species of *Mycosphaerella* also have *Cylindrosporium* imperfect stages. On the other hand, there are several form-species of *Cylindrosporium* whose perfect stages have not been found. Such are *Cylindrosporium pomi* on apple, *Cylindrosporium chrysanthemi* on chrysanthemum, and *Cylindrosporium humuli* on hops.

form-order MONILIALES

The Moniliales constitute the largest single form-order of the Deuteromycetes, encompassing over 10,000 form-species. Many of the Moniliales are of immense importance to us. In this group most of the fungal pathogens of man are classified; in this group many of the industrially important fungi belong. Among the latter are species of *Penicillium* and *Aspergillus* which are not known to form cleistothecia (*Penicillium roqueforti*, *Penicillium notatum*, *Penicillium*

chrysogenum, *Aspergillus flavus*, *Aspergillus niger*, etc.). We have already discussed these under the Ascomycetes because their characteristically shaped conidiophores leave little doubt as to their ascomycetous affinities. The so-called false yeasts, yeasts which are not known to produce ascospores, are also classified in the Moniliales under several form-families. In the Moniliales too are a number of serious plant pathogens and some common contaminants of the microbiological laboratory, as well as many soil fungi which are saprobic and may play a significant part in soil economy.

The Moniliales are variously subdivided into form-families. The number of families varies considerably and depends chiefly on whether the author includes the human pathogens and the false yeasts in the Moniliales. Differences of opinion are great, and few authors agree. The system followed in this book includes the four usually accepted form-families of mycelial fungi (Moniliaceae, Dematiaceae, Stilbellaceae, and Tuberculariaceae) and one family of false yeasts, the Cryptococcaceae. In his *Manuale de Micologia Medica*, Ciferri (1958, 1960) recognizes six families of asporogenous yeasts. Lodder, Sloof, and Kreger-van Rij (1958), as well as most other students of the yeasts, include the Sporobolomycetaceae in the false yeasts. However, the work of Nyland (1948), that of Laffin and Cutter (1959), and that of Sowell and Korf (1960/1962) leave little doubt that these fungi are Basidiomycetes. I am, therefore, treating this family under the Heterobasidiomycetidae in Chapter 20.

form-family CRYPTOCOCCACEAE

This form-family includes a number of false yeasts belonging to such form-genera as *Cryptococcus*, *Torulopsis*, and *Brettanomyces*, as well as form-genera of yeast-like fungi, such as *Candida* and *Trichosporon*, which form mycelium. Some of the yeasts have been used for food, particularly by the Germans during World Wars I and II, and are still being grown for food purposes in some places. The protein and vitamin content of most yeasts is high, and the cost of growing them is low. *Cryptococcus neoformans* is the cause of the human disease known as cryptococcosis, which may take the form of a pulmonary disease or more commonly a disease of the central nervous system designated as *Cryptococcus meningitis*. This form of the disease is the more serious by far, as it may lead to mental disorders. An ascus stage for this organism has been reported on several occasions, for example, by Dr. Rhoda Benham in 1956 in a

strain isolated from the brain of a dog. Dr. Benham pointed out the probable relation of the ascus stage to the ascosporogenous genus *Lipomyces*. In 1958, Ciferri described this species as *Lipomyces neoformans*, which now becomes the valid name of the causal agent of cryptococcosis.¹

Pityrosporum ovale, the much advertised "bottle bacillus," which is frequently associated with a dandruff condition of the scalp, is a small yeast which belongs to this form-family. Claims that it is the cause of dandruff have not been substantiated; and, according to Skinner and coauthors (1947), as well as later literature, such reports must be considered erroneous.

Rhodotorula, another genus in the Cryptococcaceae (some authors separate it in a family of its own: Rhodotorulaceae), is easily recognized. As the name indicates, it produces pink, red, or orange colonies. The genus is of no economic importance. It is often encountered as a contaminating organism in the microbiological laboratory.

Turning to the mycelium-forming members of this form-family, we must briefly consider two form-genera, *Candida* and *Trichosporon* (Figure 143). *Candida* is more yeast-like in that it normally reproduces by budding, the buds originating either from single cells or from mycelial hyphae which the organism forms under certain conditions. When grown on corn-meal agar, *Candida albicans* produces a much-branched mycelium, from which yeast-like cells (blastospores) bud profusely and from which chlamydospores also arise. Normally saprobic, this ever-present fungus sometimes turns pathogenic and causes candidiasis, a human disease which may take a number of forms. Conant and coauthors (1954) recognize the following types of candidiasis: candidiasis of the mucous membranes, cutaneous candidiasis (an infection of the skin, nails, etc.), bronchopulmonary candidiasis, and pulmonary candidiasis, which is probably the most serious form of all. It appears that the incidence of candidiasis is on the increase. This is at least partly attributed to the ever-increasing use of antibiotics which kill both beneficial and harmful bacteria in the human body and probably create conditions under which *Candida albicans* becomes pathogenic.

Trichosporon beigeli causes trichosporiasis, also called "white piedra," a disease of the beard and moustache. The treatment recommended: shave it off!

¹ Kreger-van Rij (1961) does not accept this name and makes no mention of an ascospore stage for this organism.

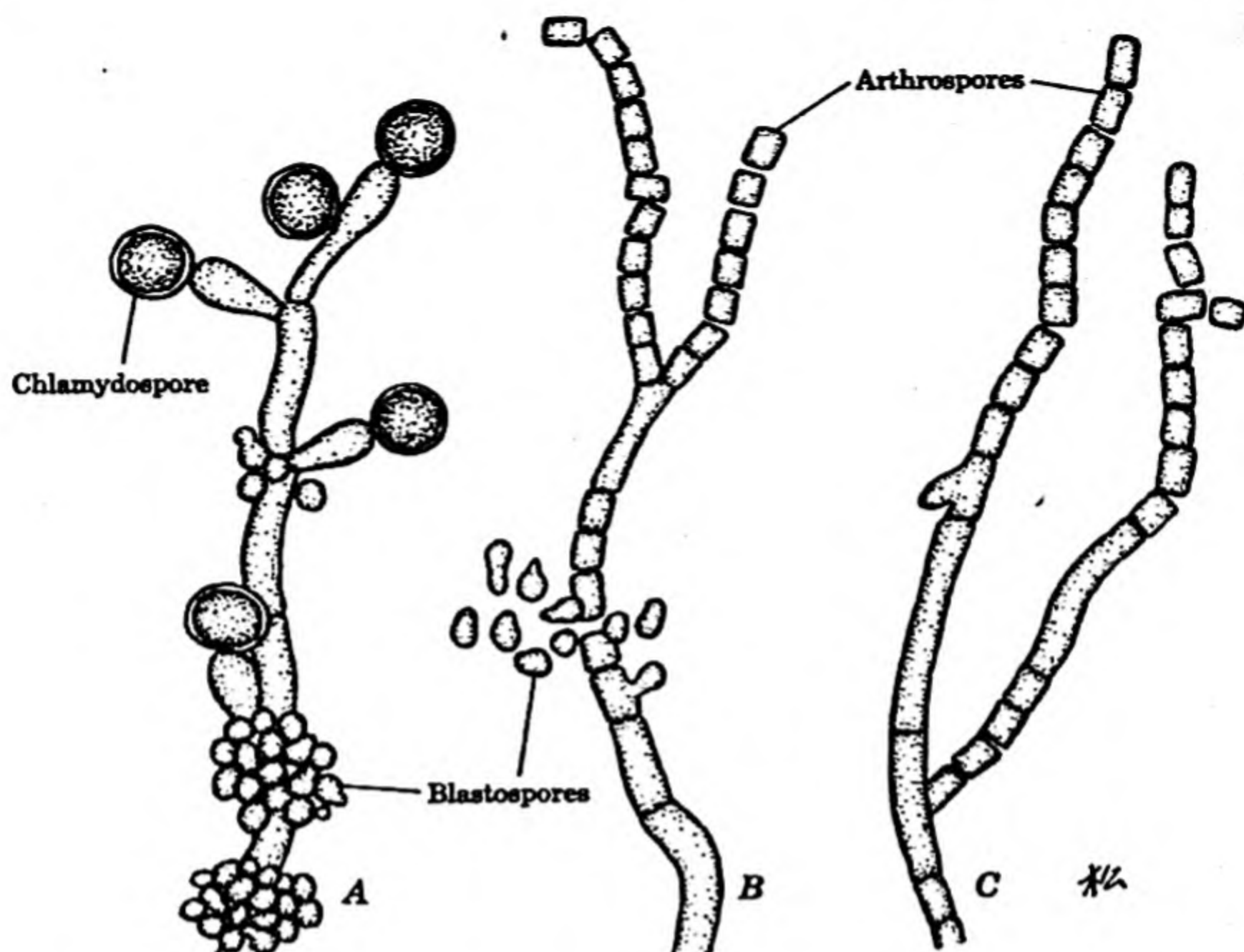


Figure 143. A. *Candida albicans*. B. *Trichosporon beigeli*. C. *Geotrichum* sp.

form-family MONILIACEAE

This form-family is the largest of all in the Moniliales. It includes all imperfect fungi which produce conidia on unorganized, hyaline conidiophores or directly on hyaline hyphae. Most species are saprobic, but many are well-known plant parasites, animal predators, or human pathogens. *Aspergillus* and *Penicillium* belong here (Figures 100A, B; 104); also the imperfect stages of the Erysiphaceae (powdery mildews) (Figure 109B), which we place in the form-genus *Oidium*. The imperfect stages of *Monilia* (Discomycetes, Helotiales, Sclerotiniaceae) belong to the form-genus *Monilia*, and those of the related genus *Botryotinia* are classified in the form-genus *Botrytis*. In *Monilia* (Figures 113C, 120B), spherical, oval, or lemon-shaped, hyaline conidia are produced in chains which are often branched; in *Botrytis* (Figure 144A), the rather large, oval or spherical conidia are produced at the tips of erect conidiophores which are simple or branched. The conidia are not in chains, but rather in head-like formations and are attached singly on sterigmata. They may be hyaline or, in some form-species, brightly colored. There are a number of form-species of *Botrytis* whose perfect stages

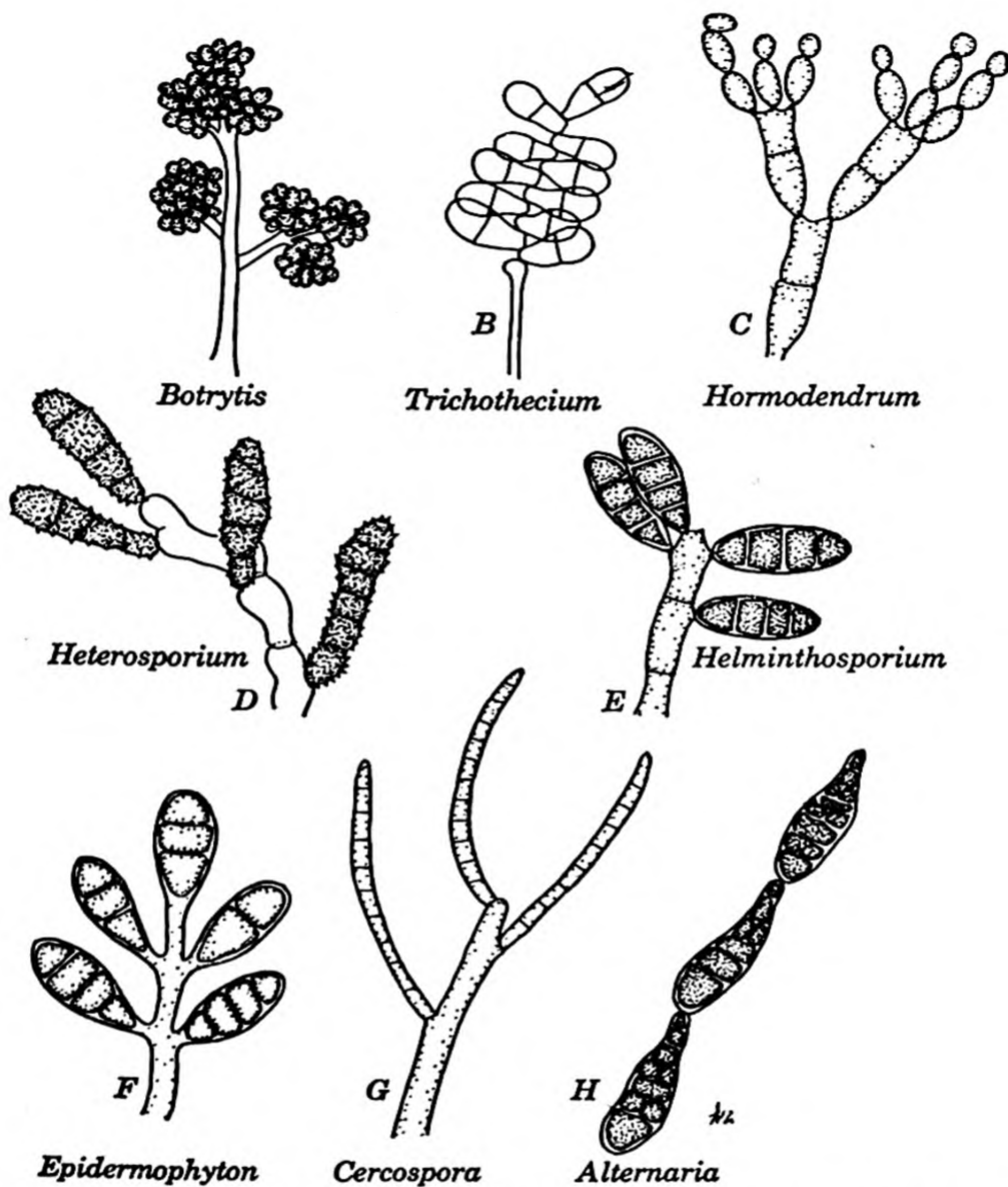


Figure 144. Conidia of some common form-genera of the Moniliales. *B*, redrawn from Ingold, 1956, *Trans. Brit. Mycol. Soc.*, 39:460–464; *D*, adapted from Jacques, 1941, *Studies in the genus Heterosporium*, Institute of Botany, University of Montreal.

are not known. Two examples are *Botrytis tulipae*, which causes a serious blight of tulips, and *Botrytis peoniae*, which causes great damage to peonies.

Verticillium (Figure 79D), with small, hyaline conidia borne on whorled (verticillate) branches, is the cause of wilt disease in many plants. *Verticillium albo-atrum* is the most common form-species. *Trichothecium roseum* (Figure 144B), the cause of pink rot of apples, generally following apple scab infection, has two-celled, ovoid conidia attached at their pointed ends to the conidiophore. The conidia are borne in chains (Ingold, 1956). They are very dilutely pigmented, appearing colorless under the microscope, but pink in masses, in culture, or on the host; this is why we call the disease "pink rot."

In the genera *Arthrobotrys*, *Dactylella*, and *Harposporium* we find the moniliaceous biological counterparts of the Zoöpagales. *Arthrobotrys* and *Dactylella* are fungi in which nature has fashioned ingenious animal traps which capture and kill nematodes. In some species (*Arthrobotrys oligospora*, *Dactylella cionopaga*, etc.) the mycelium forms sticky processes—loops or branches—to which nematodes adhere. Other hyphae then invade and digest the body of the animal.

Dactylella bembicodes forms constricting rings the cells of which swell instantly when an eelworm passes through, and hold the animal tightly until hyphal branches invade and digest it. The mechanisms by means of which fungi trap eelworms are related by Duddington (1957) in his fascinating book, *The Friendly Fungi*.

In *Harposporium*, the conidia are sticky. They adhere to an eelworm, germinate, and invade, and the internal mycelium kills and digests the animal:

Moniliaceous Human Pathogens. The Dermatophytes. The dermatophytes are fungi which cause diseases of the skin of man, animals, or both. Some, if not all, appear to survive in the soil, which thus becomes a source of infection. The diseases they cause are grouped under the general term **dermatomycoses** (sing. **dermatomycosis**; Gr. *derma* = skin) and are commonly known as ringworm, athlete's foot, etc.

Dr. Libero Ajello of the United States Public Health Service has discussed the geographic distribution of these fungi (Ajello, 1960). Of the twenty known form-species eleven are cosmopolitan, one (*Trichophyton megninii*) is strictly European, one (*Microsporum nanum*) is known only from Cuba, and one or two are endemic to Africa.

Of the four form-genera—*Epidermophyton*, *Keratinomyces*, *Microsporum*, and *Trichophyton*—to which the dermatophytes belong, the first two are monotypic, *i.e.*, consist of but a single form-species.

Epidermophyton floccosum (Figure 144F) is one of several dermatophytes causing chronic infections commonly called athlete's foot. It produces large, multiseptate, club-shaped, hyaline conidia on the somatic hyphae; there are no special conidiophores. The form-genus *Microsporum* produces very small conidia (microconidia) on its hyphae, but in addition it produces large, multiseptate, spindle-shaped macroconidia which are somewhat similar in their general aspect to those of *Epidermophyton*, just described, but are considerably larger. Five species are recognized. *Microsporum* generally infects the scalp of children, more rarely of adults, causing a condition called by members of the medical profession *tinea capitis*. *Microsporum audouini* usually occurs in epidemics, according to Dubos (1948). The form-genus *Trichophyton*, also a cause of athlete's foot and other skin ailments, is the largest of the form-genera of dermatophytes, and contains some thirteen form-species variously distributed over the world. The microconidia are the more prevalent spore form in culture, but elongated, thin macroconidia are sometimes produced. These are hyaline and multiseptate.

The perfect stages of several of the dermatophytes have now been found. Most of them belong to the Gymnoascaceae, under which we have already mentioned them.

The Agents of Deep Mycoses. Deep mycoses are diseases of the human body which affect tissues below the outer skin and which are usually chronic and serious in their effects. For a complete discussion of these diseases you must consult the medical mycology books which treat them in detail. Here we can only mention some of the fungi which are responsible for causing the diseases.

The pathogenic aspergilli and penicillia have already been mentioned in our discussion of the Eurotiales (Plectomycetes). Other form-genera of the Moniliaceae which include serious human pathogens are *Blastomyces*, *Histoplasma*, *Geotrichum*, and *Sporotrichum*.

Blastomyces dermatitidis causes North American blastomycosis. There are two forms of the infection: a localized form of mild skin disease and a severe generalized form of a pulmonary nature. The latter damages the lungs and sometimes shows symptoms similar to those of tuberculosis.

South American blastomycosis caused by *Blastomyces braziliensis* is confined to South America and some parts of Central America. Like its North American counterpart, it has a localized phase which

is confined to the skin and mucous membranes around and in the mouth, and a generalized phase which goes deeper and attacks the gastrointestinal tract. *Blastomyces brasiliensis* is also called *Paracoccidioides brasiliensis*. Ciferri (1951) proposed the family Paracoccidioidaceae, which he placed in the Entomophthorales. Later, Ciferri and his coworkers (1956) described the genus *Loboa* for *Loboa lobo*, an organism which causes a disease similar to South American blastomycosis, but which is confined to the Amazon valley of Brazil. They called this disease Lobo's disease or keloid blastomycosis and placed the genus *Loboa* in the Paracoccidioidaceae.

Histoplasma capsulatum is a moniliaceous fungus which in culture forms warty chlamydospores at the tips of the hyphal branches. It is the cause of histoplasmosis, a very widespread and serious disease which is often fatal. Like many of the human pathogens, *Histoplasma capsulatum* is a polymorphic organism exhibiting a mycelial and a yeast-like phase of growth. Emmons (1949) has repeatedly isolated the organism from the soil, and it is now fairly well established that the soil is an important source of infection, not only for this ailment but for many mycoses. The organism is separated from the Moniliaceae by some mycologists into the family Histoplasmaeae.

Geotrichum (Figure 143C) produces a well-developed mycelium. The terminal portions of its hyphae break up into short arthrospores of characteristic shape. We may describe these as cuboid or short cylindrical, with flattened ends. Certain form-species of *Geotrichum* are known to be pathogenic to man. Conant and coauthors (1954) state that four forms of geotrichosis (the disease caused by members of this form-genus) have been described: oral, intestinal, bronchial, and pulmonary. *Geotrichum candidum* is a common mold frequently associated with the molding of foods which contain lactic acid. It is particularly noticeable on pickle brine over which it forms a white, skin-like growth (pellicle). It is also found in silage, sauerkraut, and similar preparations, as well as in various dairy products. Butler (1960) has shown that *Geotrichum candidum* is pathogenic to the ripe fruits of tomato, peach, watermelon, and muskmelon. He states that the organism is responsible for a field rot of muskmelon in California. Beneke (1957) names the same species as the cause of *Geotrichosis* in man. It would be interesting to determine whether isolates from a human host would infect fruits.

Sporotrichum is another moniliaceous form-genus of medical importance because *Sporotrichum schenkii* is the cause of sporotrichosis in man and animals. This is a chronic infection which sometimes assumes epidemic proportions. The organism is normally a saprobe

on plant materials but becomes pathogenic to the human body if it enters through a wound. About forty species of *Sporotrichum* have been described, but *Sporotrichum schenkii* appears to be the only pathogenic one.

form-family DEMATIACEAE

In the Dematiaceae, both the hyphae and the conidia are typically dark, but sometimes the hyphae alone or the conidia only are dark. Here again the majority of forms are saprobic, but some are plant parasites and a few are parasitic on animals and man. In the Amerosporae, the form-genus *Hormodendrum* (Figure 144C), has very much branched, tree-like conidiophores bearing small, spherical, or oval conidia in chains. Various form-species are often found contaminating Petri dish cultures in the laboratory. *Hormodendrum pedrosoi* and *Hormodendrum compactum* cause chromoblastomycosis, a skin disease in which masses of warty tissue are formed over the infected portions of the body, usually the legs, feet, arms, and hands.

Cladosporium is a form-genus with two-celled, dark conidia. It contains a large number of saprobes which are found on dead plant tissues. A few form-species, however, are serious plant parasites. *Cladosporium carpophilum* causes peach scab, and *Cladosporium fulvum* is the cause of the serious tomato leaf mold to which greenhouse tomato plants are particularly susceptible. Many authors consider *Hormodendrum* and *Cladosporium* synonymous.

In the Phragmosporae, *Heterosporium* and *Helminthosporium* are the most common form-genera (Figures 144D, E). The conidia are large and multiseptate in both: in the former they are spiny; in the latter, smooth. *Heterosporium iridis* (the imperfect stage of *Didymella iridis*) is the cause of the very common and often very destructive iris leaf spot. Several Ascomycetes have imperfect stages of the *Helminthosporium* type which cause very destructive diseases of cultivated crops. Among these are *Pyrenophora teres* (= *Helminthosporium teres*), the cause of net blotch of barley; *Pyrenophora graminea* (= *Helminthosporium gramineum*), the cause of leaf stripe of barley; and *Ophiobolus sativus* (= *Helminthosporium sativum*), the cause of foot rot of barley. There are also many form-species of *Helminthosporium* whose perfect stages have not been found.

The form-genus *Alternaria* is the most commonly encountered of the Dictyosporae (Figure 144H). The conidia are rather large and are multicellular with both transverse and longitudinal septa occur-

ring typically. The conidia are usually borne in chains, but not infrequently they are formed singly at the tips of the hyphae which bear them. Actually no conidiophores here are distinguishable from the somatic hyphae. *Alternaria* occurs universally. Several form-species are found as saprobes on dead and dying plant parts and in the soil from which the conidia are picked up by the wind, and invade laboratories, where they are troublesome as contaminants of cultures. *Alternaria* conidia also occur abundantly in house dust and have been found to be the chief fungal causes of hay fever. Some form-species are parasitic on plants. *Alternaria solani* causes early blight of potatoes (not to be confused with late blight due to *Phytophthora infestans*).

The form-genus *Cercospora* (Figure 144G) of the Scolecosporae should finally be mentioned. This form-genus contains about 3800 described form-species (Chupp, 1953), many of which are destructive plant parasites, causing leaf spots. Studies on pathogenicity and cultural characters (Johnson and Valleau, 1949) indicate, however, that many of these form-species are actually the same fungus attacking different hosts and described many times under different



Figure 145. Patient with face lesions from which *Cercospora apii* was isolated. Courtesy Emmons *et al.*, 1957, *Mycologia*, 49:1-10.

names (sparrow in a pear tree . . . !). *Cercospora apii*, which was first described as the cause of a destructive celery leaf spot, has been found, according to these investigations, to be pathogenic also to beet, tobacco, and several other crops on which it causes serious leaf spots. More startling is the report that this same organism may be a human pathogen (Emmons *et al.*, 1957). It was isolated from a severely infected patient in Indonesia (Figure 145), cultured on agar media, and inoculated on various species of plants. *Cercospora* leaf spots developed on lettuce, tomato, and potato seedlings, and the fungus, indistinguishable from that isolated from the human patient, was recovered from the diseased plants.

form-family STILBELLACEAE

The conidiophores of fungi which we place in this form-family are united into synnemata. The majority of these forms are saprobic. The form-genus *Graphium* is of economic significance because several of its form-species are responsible for blue stain of lumber, which reduces its market value. The imperfect stage of *Ceratocystis ulmi* (= *Graphium ulmi*) also belongs here.

form-family TUBERCULARIACEAE

The characteristic structure of the Tubulariaceae is a sporodochium, which has been described in connection with the discussion of *Nectria cinnabarina* (= *Tubercularia vulgaris*) on pages 318-320. There are 152 form-genera listed by Bender (1931) in this form-family. Of these, *Tubercularia*, *Volutella*, and *Fusarium* are the best known. In *Tubercularia* the sporodochium is generally shaped like a mushroom, with a very short stalk and a smooth surface. In *Volutella* the sporodochium produces setae arising here and there over the entire fructification. *Volutella fructi* causes dry rot of apples. The form-genus *Fusarium* is the largest in the Tubulariaceae and, taxonomically, one of the most difficult of all fungal groups. Few mycologists attempt to identify form-species of *Fusarium* because of the great variability they encounter in this group, a variability which makes identification uncertain for all but the few specialists. *Fusarium* produces long, crescent-shaped, multiseptate macroconidia typically borne on sporodochia, and very small, spherical, oval, elongated, or crescent-shaped microconidia on simple or branched single hyphae. Chlamydospores are also commonly produced by the mycelium, and sclerotia are often formed. Parasitic fusaria are gen-

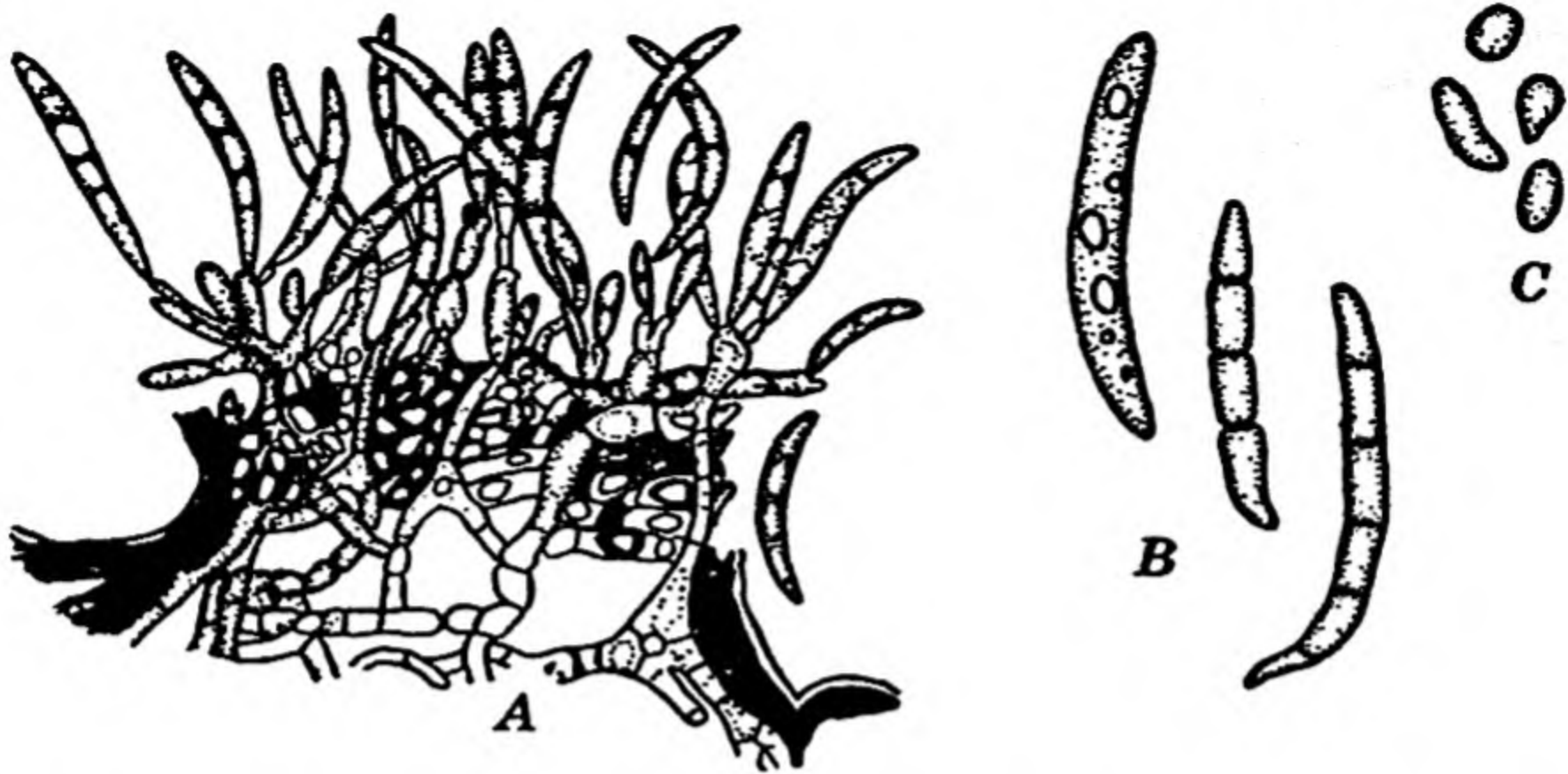


Figure 146. A. Sporodochium of *Fusarium lini*. B, C. *Fusarium* sp. B. Macroconidia. C. Microconidia. Redrawn from Bolley, 1901, *North Dakota Bull.*, 50:25-58.

erally vascular parasites causing wilts of plants by plugging the conducting tissues and by toxin secretions as well. Among the most destructive form-species are *Fusarium solani* on potato, *Fusarium lini* on flax (Figure 146), and *Fusarium oxysporum* var. *cubense* on banana. The last species causes the notorious Panama disease, which is crippling the banana-growing industry in Central America.

form-order MYCELIA STERILIA

Of the twenty or more form-genera in this conglomerate assemblage, *Rhizoctonia* and *Sclerotium* are the best known and the most widely distributed. *Rhizoctonia* is commonly found in soils, causing damping-off and root rot of various host plants. *Pellicularia filamentosa*, a basidiomycete, has *Rhizoctonia solani* as its imperfect stage. It causes black scurf of potatoes, a serious disease of the tubers, and attacks numerous other plants both cultivated and wild.

Sclerotium cepivorum, known only in the form of small black sclerotia produced on white, cottony hyphae, causes white rot of onions and garlic. *Sclerotium rolfsii* is an omnivorous and destructive parasite of many plants.

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19 class

BASIDIOMYCETES

smuts, rusts, jelly fungi, mushrooms,
puffballs, and stinkhorns

Introduction. We classify an immense variety of fungi in this, the most advanced of all fungal classes. The true Basidiomycetes consist of forms which people call mushrooms, toadstools, puffballs, and stinkhorns. The so-called shelf fungi or bracket fungi also belong here, as well as the less familiar bird's-nest fungi. The smuts, the rusts, and the jelly fungi are also Basidiomycetes, constituting what is probably a group more primitive than the higher Basidiomycetes.

The Basidiomycetes differ from all other fungi in that they produce their spores, called basidiospores, on the outside of a specialized, spore-producing body, the basidium. Basidiospores are generally uninucleate and haploid. Like ascospores, they are the result of plasmogamy, karyogamy, and meiosis, the last two of which occur in the basidium. Thus, a definite number of basidiospores, usually four, is typically produced on each basidium. Many students of these fungi regard the basidiospores as homologous to ascospores, since both types develop in a comparable manner, and the Basidiomycetes are thought to have originated from the Ascomycetes.

Occurrence, and Importance to Man. From our standpoint, the Basidiomycetes are an important group of fungi including many harmful species as well as some useful ones. Beginning with the smuts and rusts, we have two groups of parasites causing plant diseases which destroy several million dollars' worth of crops annually. Notorious among these diseases are stinking smut and black stem-rust of wheat. There are many others which attack a large variety of food and ornamental plants. The higher Basidiomycetes are significant in causing diseases of forest and shade trees and in destroy-

ing lumber, railroad ties, etc. In the tropics, where the atmospheric humidity is high at all times, it was not uncommon some years ago to see old model-T's with fruiting bodies of shelf fungi growing from the wooden skeletons of the car tops. Business spends thousands of dollars annually for preservatives to protect lumber from the attacks of these and other fungi. One of the big items in railroad operation is a periodical inspection of railroad ties which are weakened by wood rots, the result of invasion by basidiomycete mycelium. Railroads sometimes employ mycologists for the purpose of keeping up with the latest developments in the field of wood preservatives.

Many Basidiomycetes are eagerly sought as food by mushroom-lovers the world over. The cultivation of mushrooms for food has developed into an industry of considerable proportions in the United States, and is continually growing. Although only one species of mushroom (*Agaricus campestris bisporus*) is cultivated extensively for food, many of the wild species are equally good or better in flavor, and are highly prized by connoisseurs. We shall say more about mushroom eating in Chapter 21 when we discuss the order Agaricales.

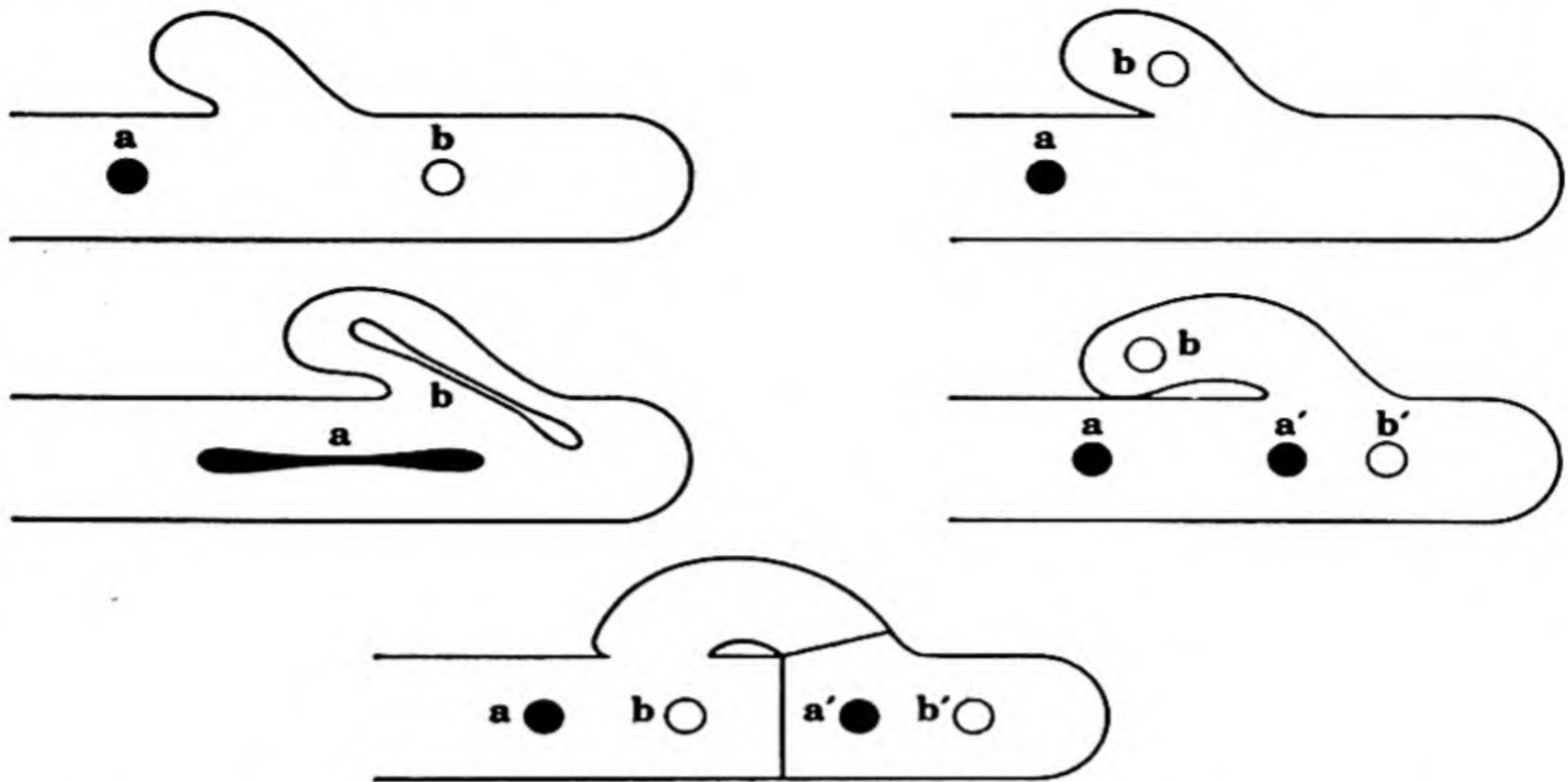
Somatic Structures. The mycelium of the Basidiomycetes consists of well-developed, septate hyphae which penetrate into the substratum and absorb nourishment. Individually, the hyphae are microscopic, but you can plainly see them in mass, as mycelium, without the aid of a lens. You can find basidiomycete mycelium if you look in moist places in the woods, on rotten logs—mostly under the bark—on wet, dead leaves, or on other organic matter. The mycelium is usually white, bright yellow, or orange, and often spreads out in a fan-shaped growth. In some forms, a number of hyphae lying parallel to one another are joined together to form thick strands of mycelium, commonly called shoe strings, which, technically, we term rhizomorphs. These strands are enveloped in a sheath or cortex and behave as a unit or tissue.

The mycelium of most Basidiomycetes passes through three distinct stages of development, the primary, the secondary, and the tertiary, before the fungus completes its life cycle. The primary mycelium usually develops from the germination of the basidiospore. It may be multinucleate at first, the nucleus or nuclei of the basidiospore dividing many times as the germ tube emerges from the spore and begins to grow. Such a multinucleate phase of the primary mycelium is short, however, because septa are soon formed which divide the mycelium into uninucleate cells. In some species, septum formation begins upon completion of the first division of the spore nuclei

(Bakerspigel, 1959) so that the primary mycelium is septate and uninucleate from the beginning.

The secondary mycelium originates from the primary mycelium. Its cells are typically binucleate. The binucleate condition begins when the protoplasts of two uninucleate cells fuse, without karyogamy taking place after plasmogamy. The binucleate cell thus formed produces a branch into which the nuclear pair migrates; the two nuclei divide conjugately and the sister nuclei separate into the two daughter cells, thus initiating the binucleate mycelium.

The binucleate mycelium may be initiated in another fashion (Raper, 1953). The two nuclei from mycelia x and y in the original dikaryotic cell formed by plasmogamy may divide, and a daughter nucleus of each may migrate through the septal pore into the adjacent cells. The x nucleus enters the cell of the y mycelium, and the y nucleus invades the cell of the x mycelium. The foreign nucleus in each mycelium now divides rapidly, and its progeny migrate from cell to cell until both parent mycelia have been completely dikaryotized. An interesting mechanism found in all major types of Basidiomycetes, but not in all species, operates to ensure that sister nuclei arising from conjugate division of the dikaryon become separated in the two daughter cells. This mechanism functions through special structures we call **clamp connections**, which are formed during nuclear division. When a binucleate cell is ready to divide, a short branch—the clamp connection—arises between the two nuclei a and b and begins to form a hook. The nuclei now divide simultaneously. One division becomes oriented obliquely so that one daughter nucleus b forms in the clamp connection and the other b' forms in the dividing cell. The second division orients itself along the long axis of the dividing cell, so that one daughter nucleus a forms near one end of the cell and the other a' approaches the nucleus b' of the first division near the other end of the cell. In the meantime, the clamp has bent over, and its free end has connected with the cell, so that the clamp forms a bridge through which one of the daughter nuclei b passes to the other end of the cell and approaches one of the daughter nuclei a of the other division. A septum forms to close the clamp at the point of its origin and another septum forms vertically under the bridge, to divide the parent cell into two daughter cells with nuclei a and b in one daughter cell and nuclei a' and b' in the other as shown in the following series of diagrams.



Of great interest is an electron microscope study of the septa of the Ascomycetes, Deuteromycetes, and Basidiomycetes, made by Moore and McAlear (1962). This study revealed that, whereas the septa of the first two groups are perforated in a simple manner (Figures 78, 137) as had been observed by the light microscope, those of the secondary mycelium of some Basidiomycetes appear to be very different in structure (Figure 147).

Longitudinal sections through the dikaryotic hyphae of five species of Basidiomycetes, distributed among four families, two in each of the sub-classes, reveal that the septum is a cross-wall which flares out in the middle portion of the hypha, forming a barrel-shaped structure with open ends. Moore and McAlear call this type a **dolipore septum** (*L. dolium* = large jar). The electron microscope further reveals a curved double membrane on each side of the septum. Because this membrane structure looks like a parenthesis, in section, it has been designated as a **parenthesome**. If the parenthesomes are continuous structures, it would appear that they form two cups around the open ends of the barrel and, in so doing, may block the passage of nuclei from one cell to the next through the central pore, permitting, perhaps, cytoplasmic continuity, as do the simple septa of the Ascomycetes, which, however, also permit nuclei to pass through.

The significance of this septal apparatus in the dikaryotic mycelium of the few Basidiomycetes which have been investigated up to now

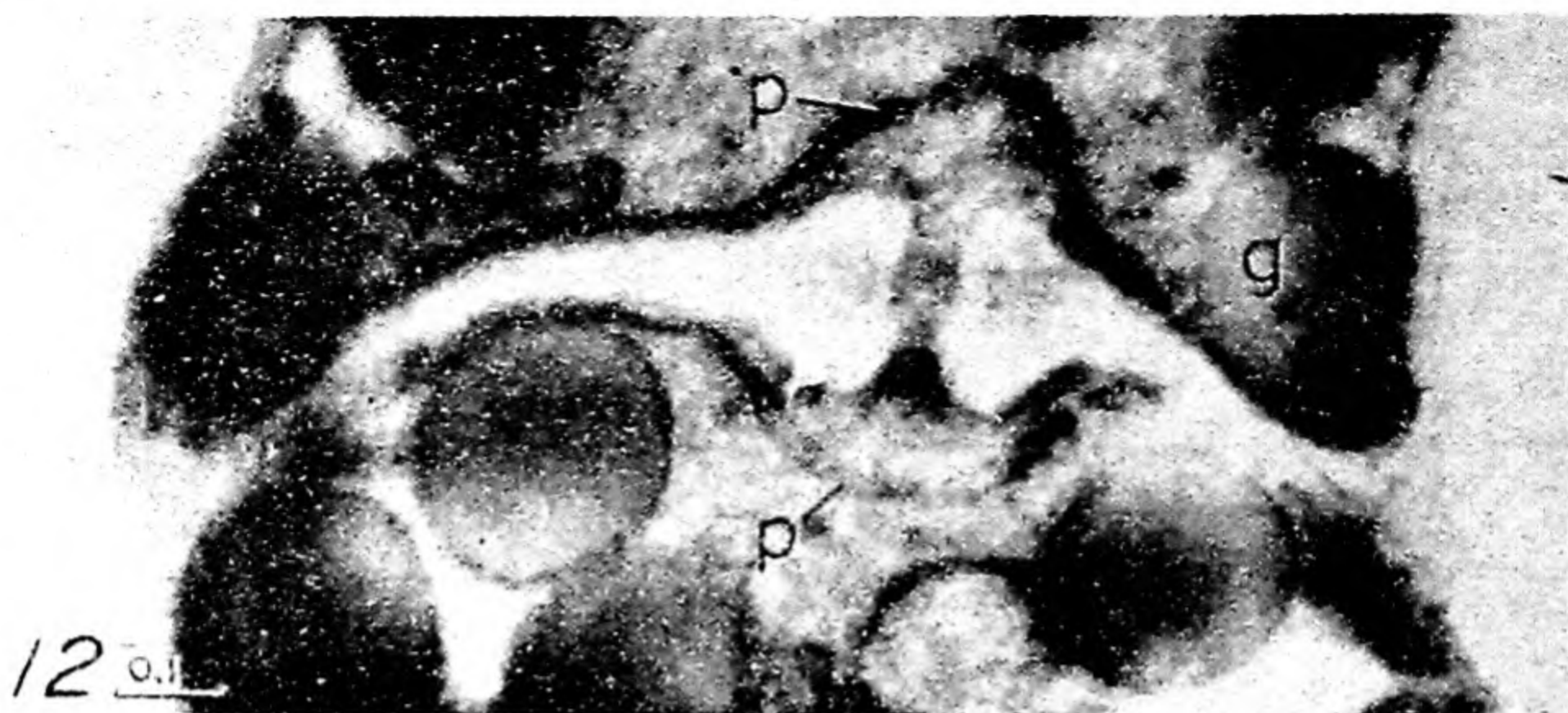


Figure 147. Dolipore septum and parenthesomes (p) of the dikaryotic mycelium of *Auricularia auricula*. Courtesy Moore and McAlear, 1962, *Am. Jr. Bot.*, 49:86-94.

is difficult to evaluate until we obtain information about the septal structure of the primary mycelium of the same fungi, the relative occurrence of the dolipore septum throughout the class Basidiomycetes, and the occurrence and structure of clamp connections in the mycelia that possess this type of septum.

The occurrence of clamp connections, and their relationship to the binucleate condition of the basidiomycete secondary mycelium, have prompted some mycologists to liken these structures to the hooks of the ascogenous hyphae in the Ascomycetes. The fact that a clamp generally occurs at the base of a basidium, which typically arises from a binucleate hypha, somewhat strengthens this view.

Be that as it may, the binucleate mycelium of the Basidiomycetes—arising typically as it does as a result of plasmogamy, and giving rise eventually to the basidium in which karyogamy and meiosis occur—is certainly analogous to the ascogenous hyphae from which the asci arise. Whether the two are homologous as well is another question.

The tertiary mycelium is represented by the organized, specialized tissues which compose the sporophores of the higher Basidiomycetes. The cells of the tertiary mycelium are binucleate, the sporophores actually originating when the secondary mycelium forms complex tissues.

Thus, the basidium, the dikaryotic mycelium, the formation of clamp connections and, possibly, the dolipore septum/parenthesome mechanism are the typical characteristics of the Basidiomycetes.

Yet these characteristics are not so clear-cut as they appear to be as you read the above statement. In the rusts and smuts, for example, the basidium is considerably different from what we consider the typical basidium to be. It begins as a heavy-walled spore which serves as the overwintering stage of the fungus and then germinates to form a tube (promycelium) on which the basidiospores are produced. Functionally and cytologically, the mechanism is, without question, a basidium, but morphologically it differs from that of the higher Basidiomycetes. The binucleate hyphae, which are characteristic of the Basidiomycetes, are represented by a few binucleate cells of the ascogenous hyphae of the Ascomycetes. The dikaryotic phase of the Basidiomycetes, however, not only is more extensive, but also occupies a much longer phase in the life cycle, and is biologically independent of the monokaryotic mycelium. Finally, clamp connections, which are in general characteristic of basidiomycetous mycelium, seem to be absent from many species of undoubted Basidiomycetes; yet they have been reported in the ascogenous hyphae of some Tuberales, which are undoubted Ascomycetes.

All these exceptions may seem confusing at first, but actually they should serve to unify your concept of the fungi and to reveal to you the orderly evolution of these organisms and the unfolding of one form from another.

The Basidiocarp. The higher Basidiomycetes produce their basidia in highly organized fruiting bodies of various types. These fruiting structures, corresponding to the ascocarps of the higher Ascomycetes, are called **basidiocarps** (Gr. *basidion* = small base, basidium + *karpos* = fruit). Basidiocarps may be thin and crust-like, gelatinous, cartilaginous, papery, fleshy, spongy, corky, woody, or indeed of almost any texture. They vary greatly in size from microscopic to 3 feet or more in diameter. It is within this group that fruiting bodies have reached their greatest complexity and size. Most Basidiomycetes bear their basidia in basidiocarps. However, the rusts and the smuts, belonging to the orders Uredinales and Ustilaginales, respectively, do not, except in one or two species, form any basidiocarps.

Fruiting bodies of Basidiomycetes are among the most familiar examples of fungi. Mushrooms, shelf fungi, coral fungi, puffballs, earthstars, stinkhorns, and bird's-nest fungi are all examples of basidiocarps of the fungi which bear them. The main body of the fungus in each case is the extensive mycelium, which usually goes unnoticed.

Basidiocarps may be open from the first, exposing their basidia, or

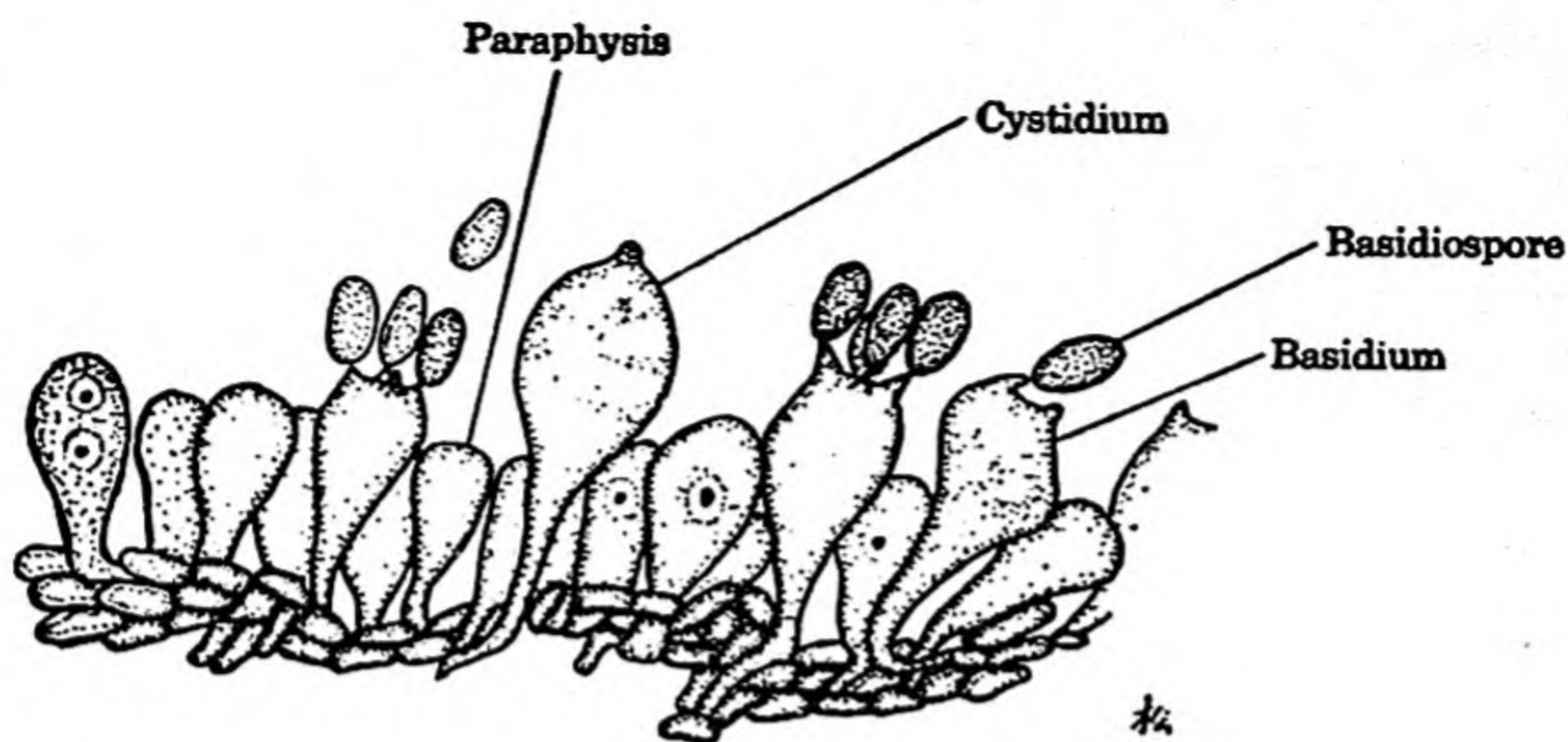


Figure 148. Hymenium of a basidiomycete.

they may open at a later stage, or even remain closed. In species whose basidiocarps remain closed the spores are liberated only upon the disintegration of the basidiocarp or upon its accidental fracture by external forces.

The basidia are typically formed in definite layers called hymenia (Figure 148), which are comparable to the layers of asci in the higher Ascomycetes. In a basidiocarp, then, the hymenium is a layer composed of basidia and perhaps sterile structures interspersed with them. Such sterile structures are often difficult to distinguish from the basidia and are then regarded as paraphyses; some mycologists regard them as immature basidia. However, some species have sterile processes among the basidia, which are very much larger than the latter and are easily distinguishable. Such structures are called cystidia (sing. cystidium; Gr. *kystis* = bladder + *-idion*, dimin. suffix). In fungi which bear their basidia exposed, the hymenium may cover the entire surface of a basidiocarp or only a portion of it, or may be confined to specialized portions of the basidiocarp. We use the method in which these fungi bear their hymenia to delimit large categories, such as families and orders in the classification of the Basidiomycetes.

The Basidium. The simple, club-shaped basidium of the higher Basidiomycetes may be regarded as the characteristic form of this structure (Figure 149). The basidium originates as a terminal cell of a binucleate hypha and is separated from the rest of the hypha by a septum over which a clamp connection is generally found. At first narrow and elongated, the basidium soon enlarges and becomes broader. While these external changes are taking place, the two

nuclei within the young basidium fuse (karyogamy), and the zygote nucleus soon undergoes meiosis, giving rise to four haploid nuclei. In the meantime, four sterigmata push out at the top of the basidium and their tips enlarge, forming the basidiospore initials. The four nuclei now squeeze through the narrow sterigmatal passage into the young basidiospores, which eventually complete their development as uninucleate, haploid cells. Typically four-spored, basidia may, however, bear from one to many spores, depending on the species.

In the lower Basidiomycetes, the basidia vary considerably from the type. Some are deeply divided, resembling a tuning fork; others are longitudinally septate; still others are transversely septate. We shall discuss these various forms under the groups of which they are characteristic.

The Basidiospore. The basidiospore is typically a unicellular, uninucleate, haploid structure. Basidiospores may be globose, oval, elongated, or sausage-shaped; colorless or pigmented. In many cases the pigments are very dilute and can be detected only when large masses of spores are deposited. Such pigments may be green, yellow, orange, ochre, pink, brown, violet-brown, or black. The darker

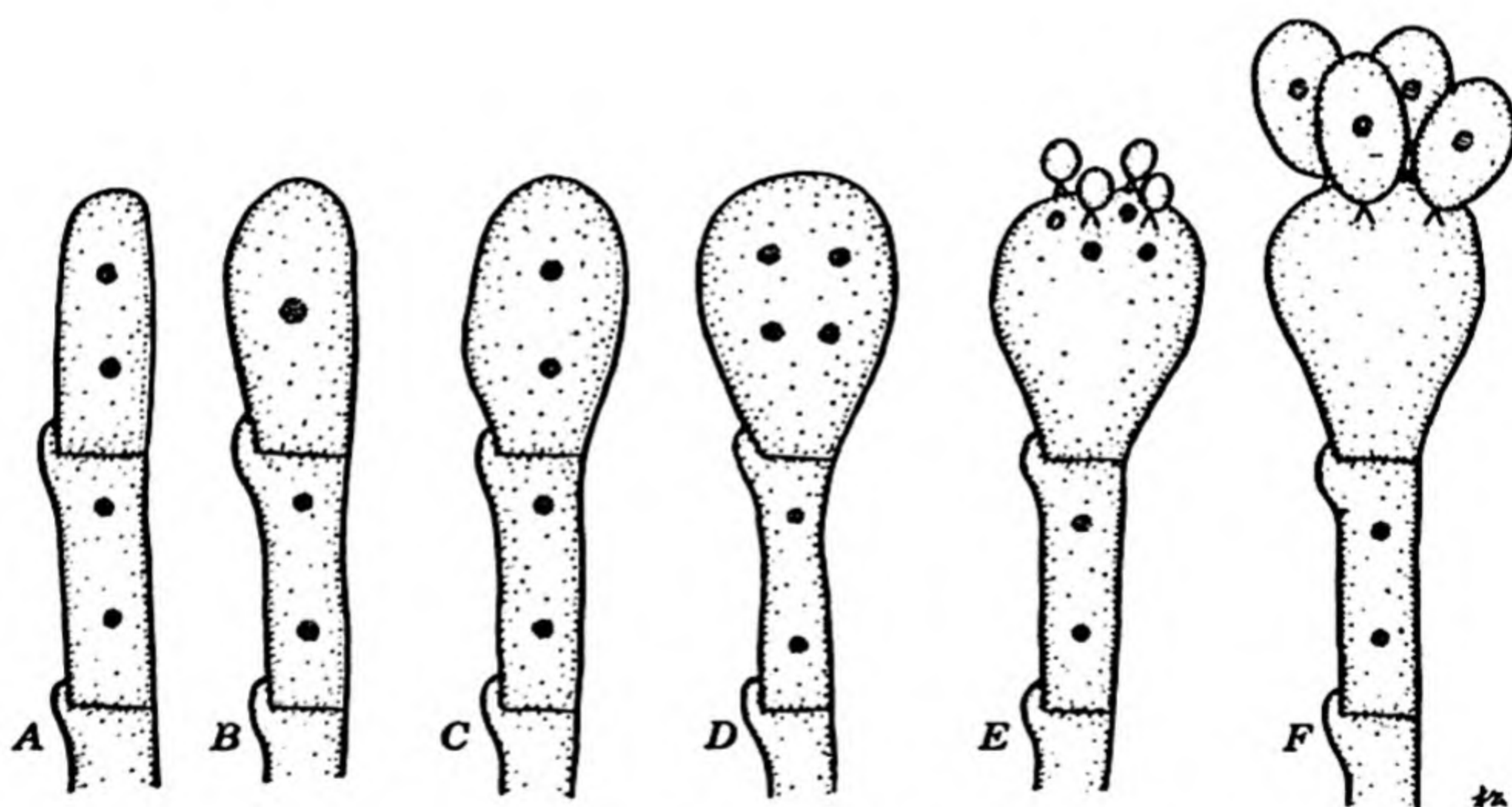


Figure 149. Six successive stages in the development of a basidium. A. Binucleate hyphal tip. B. Karyogamy. C. First meiotic division (2-nucleate stage). D. Second division (4-nucleate stage). E. Young basidiospores developing on sterigmata and nuclei preparing to migrate into the spores. F. Mature basidium with four uninucleate basidiospores.

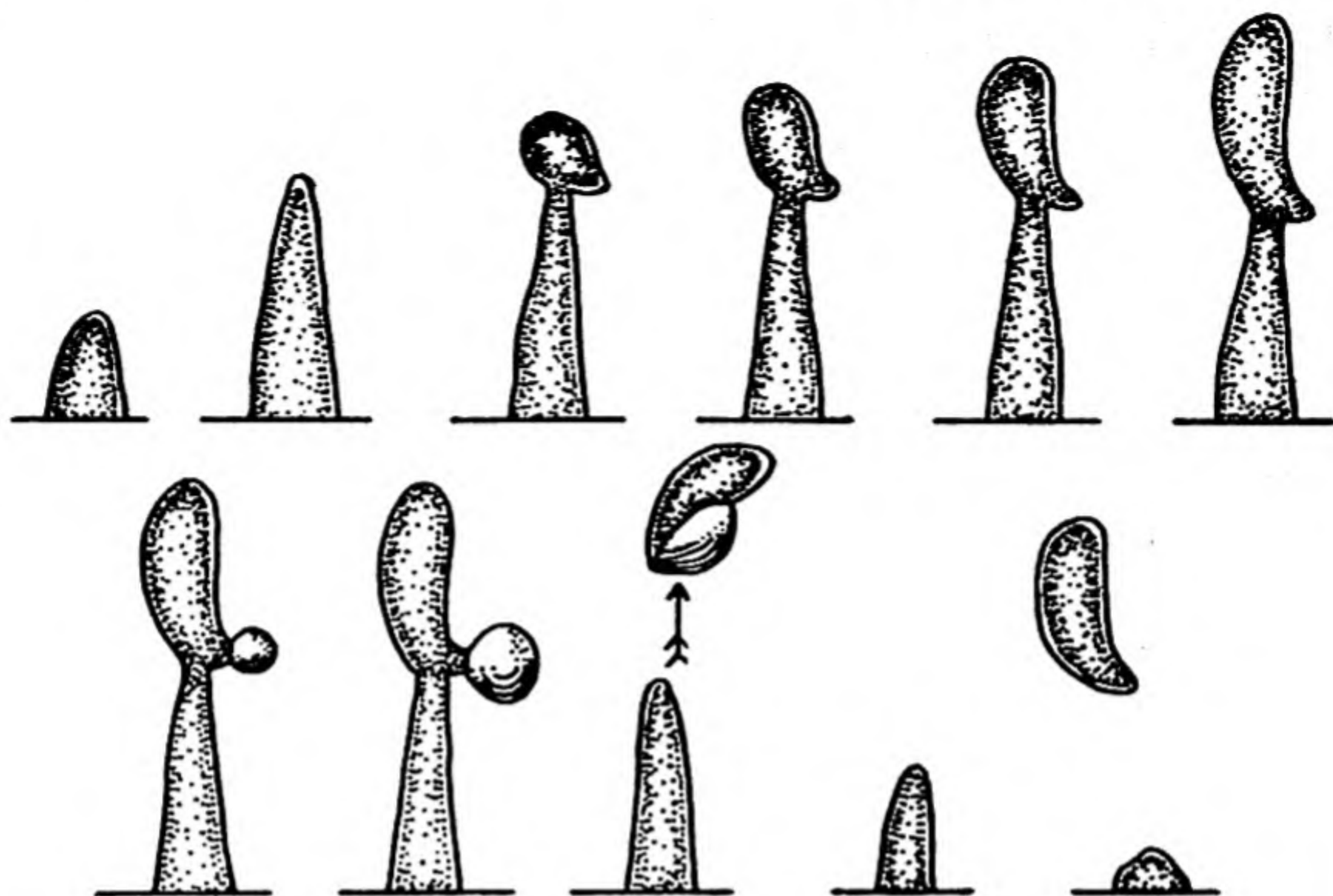


Figure 150. Basidiospore formation and discharge in *Calocera cornea*. Redrawn by permission from *Researches on fungi*, Vol. 2, by A. H. R. Buller, 1922, Longmans, Green and Company, London.

pigments can be detected in individual spores as well as in mass spore deposits, but a spore print is necessary for the recognition of the lighter pigments, these being so dilute that it is impossible to detect them in single spores under the microscope. Spore prints and the method for preparing them are discussed in Chapter 21 under the family Agaricaceae.

A basidiospore often rests on the tip of a sterigma in an oblique fashion and, in forms with exposed basidia, is discharged with force from the sterigma as a general rule. When the basidiospore matures, a droplet of water begins to form at its basal end. This droplet gradually enlarges. When it reaches a certain volume the basidiospore is shot off the sterigma, taking the droplet with it (Figure 150). The sterigma may or may not collapse after the spore is discharged. Since all the nuclei of the basidium migrate into the basidiospores, only one crop of basidiospores is produced by each basidium in most Basidiomycetes.

The basidiospores germinate in water by means of germ tubes which generally develop into uninucleate mycelia. In a number of Basidiomycetes, the basidiospores are binucleate at maturity. This may occur in one of two ways. (1) The spore may be uninucleate in origin and become binucleate by the division of its nucleus. Such

spores usually give rise to uninucleate mycelium. (2) Two of the four daughters of the zygote nucleus may be incorporated in a single basidiospore. Such spores typically give rise to binucleate mycelium. In some species a basidiospore, instead of producing mycelium, gives rise by budding to large numbers of tiny conidia from which the mycelium is formed.

Asexual Reproduction. Asexual reproduction in the Basidiomycetes takes place by means of budding, by fragmentation of the mycelium, and by the production of conidia, arthrospores, or oidia. Conidial production is common in the smuts, where conidia are budded off both the basidiospores and the mycelium. The rusts produce summer spores (uredospores) which are conidial in origin and function. Many other Basidiomycetes also produce conidia. The hyphae of Basidiomycetes often break up into unicellular sections which, without rounding up or forming thick walls, as chlamydospores do, germinate into germ tubes which develop into mycelia. These mycelial fragments are the arthrospores. They may be uninucleate or binucleate, depending on whether they are produced from primary or secondary mycelium. Oidia are produced by special, short hyphal branches, the oidiophores, which cut off oidia in succession, from the tip of the oidiophore (Figure 151). Such oidia serve a dual purpose; they may either germinate and produce uninucleate, primary mycelia, or they may act as spermatia, uniting

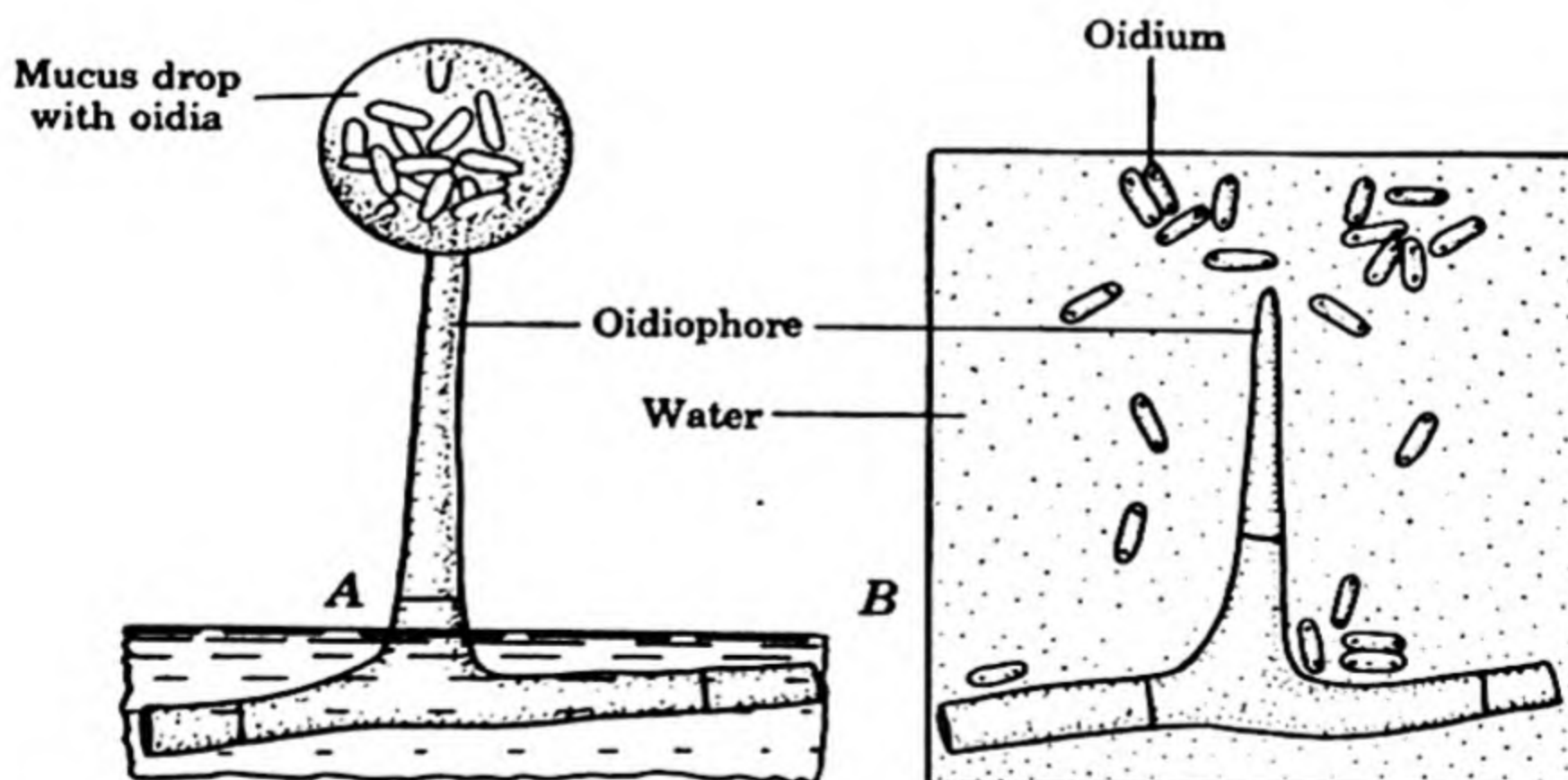


Figure 151. Oidiophore and oidia of *Coprinus lagopus*. A. In the air. B. After submerging in water. Redrawn by permission from *Researches on fungi*, Vol. 2, A. H. R. Buller, 1922, Longmans, Green and Company, London.

with somatic hyphae, thus behaving as do the conidia of *Neurospora* (Sphaeriales, Sordariaceae).

Sexual Reproduction. In the Basidiomycetes, plasmogamy is basically the means of attaining the dikaryophase (binucleate condition) from the monokaryophase (uninucleate condition). This is accomplished either by somatogamy or by spermatization. Dikaryotization through somatogamy was explained earlier (page 428). In basidiomycetous species which produce oidia, plasmogamy often takes place by the union of an oidium with a somatic hypha. The oidia, which are produced at the tips of short oidiophores, are usually enveloped in a droplet of mucus in which many oidia are held together (Figure 151). These oidia are carried by insects or water to the sides of somatic hyphae which act as receptive organs. A pore is then dissolved at the point of contact between hypha and oidium, and the oidial protoplast passes into the hyphal cell and makes it binucleate. Further development is the same as that which follows somatogamy.

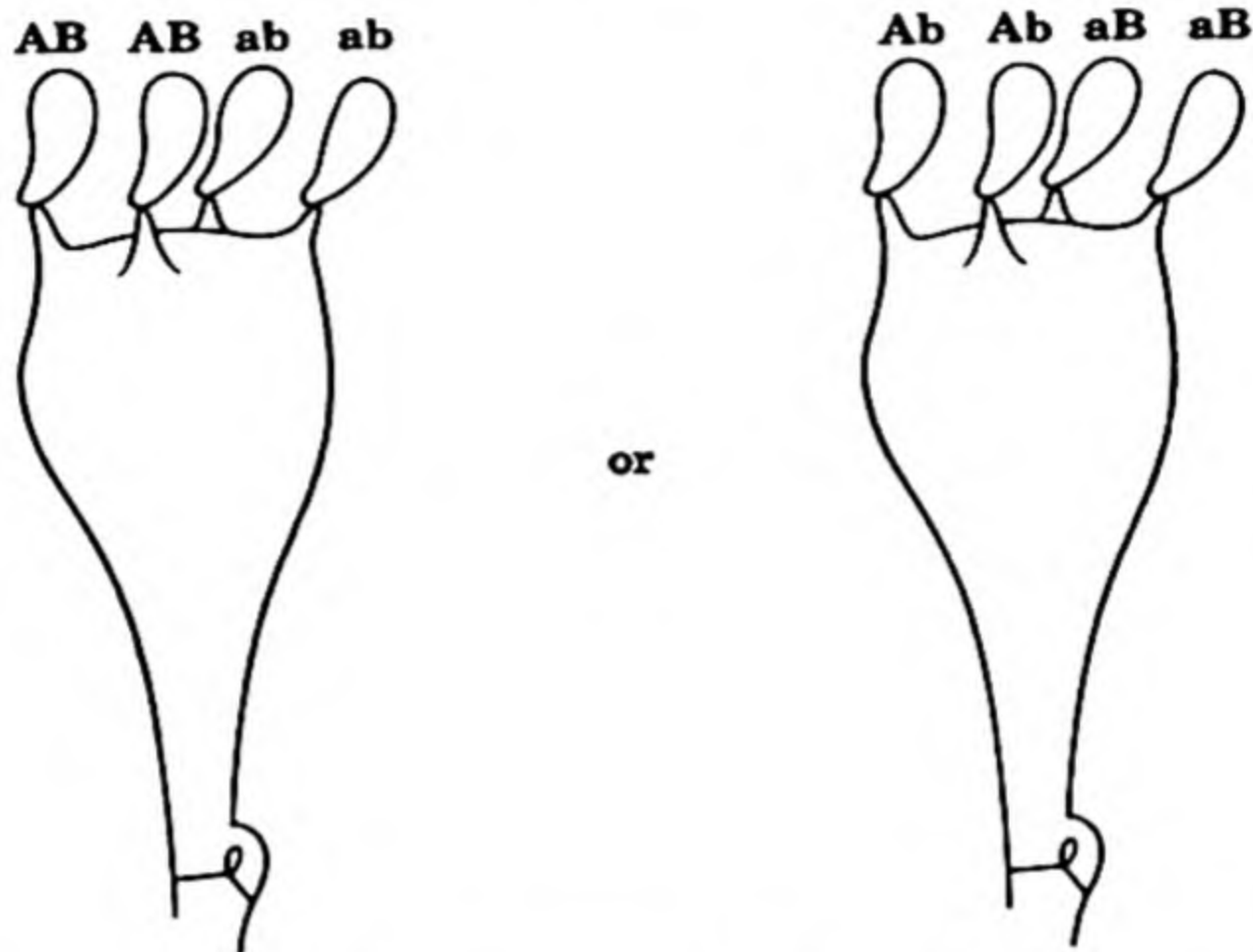
Thus, most Basidiomycetes have no sex organs at all, the somatic hyphae and detached somatic cells (the oidia) taking over the sexual function. The rusts, however, as we shall see in Chapter 20, form specialized spermatia and receptive hyphae whose sole function is sexual reproduction by spermatization.

The foregoing accounts of plasmogamy describe only the most simple and probably basic pattern. There are so many variations to this pattern, however, that to leave the subject at this point gives an oversimplified view of the situation. For a lucid presentation of the very complex subject of sex in the Basidiomycetes read Raper's (1953) article on "Tetrapolar Sexuality," and continue with Raper (1960) and Takemaru (1961).

Compatibility. As in the Ascomycetes, so too in the Basidiomycetes we have homothallic, secondarily homothallic, and heterothallic species, with about 90 per cent of all investigated species falling in the last category (Whitehouse, 1949a, b). Sexual compatibility in about 37 per cent of heterothallic species is governed by one pair of factors, Aa, located on the same locus on different chromosomes, and behaving in the same manner as do those of the heterothallic *Mucorales* or such Ascomycetes as *Neurospora sitophila* (see page 309 and Figure 113). We call such species bipolar. The remaining 63 per cent of heterothallic species are tetrapolar; i.e., sexual compatibility is governed basically by two pairs of factors AaBb located on different chromosomes and segregating independently. This means that four possible types of basidiospores are produced by tetrapolar

species: **AB**, **Ab**, **aB**, **ab**. However, whether a given basidium of a tetrapolar species will bear two kinds or four kinds of basidiospores depends on chromosome arrangement during meiosis and on crossing-over.

If no crossing-over takes place between the mating-type loci and their centromeres, then only two kinds of spores will be formed on a basidium:



If, however, crossing-over occurs for one mating-type locus, four types of spores will be formed, as follows:



If crossing-over occurs for both mating-type loci, two or four types of spores may be formed on a given basidium, depending on the

arrangement of the chromosomes on the metaphase plate at meiosis.

As Raper (1953–1960) explains in detail, further complications arise from the existence of numerous multiple alleles for each mating type, from several closely located genes which together determine mating type at each locus, etc.

In *Schizophyllum commune*, a difference has been detected (Raper and Esser, 1961) in the proteins of two compatible primary mycelia and the dikaryotic mycelium resulting from their mating. This difference appears to reflect the biochemical activity of the incompatibility factors.

In the most advanced groups of Basidiomycetes it is probable that plasmogamy no longer takes place. In many species the basidiospores are binucleate, and it appears that, upon germination, the two nuclei move into the germ tube and thereafter divide conjugately, giving rise to a binucleate mycelium. The primary mycelium has thus been dropped from the life cycle and with it the sexually functioning cells and the process of plasmogamy. Karyogamy, however, does take place in the basidium and is followed by meiosis, which results in the formation of four haploid nuclei. Instead of one nucleus migrating into a separate basidiospore, only two basidiospores are formed, each receiving a pair of nuclei from the basidium. The basidiospores of many species of the higher Basidiomycetes germinate with difficulty or not at all under laboratory conditions, and consequently studies of early developmental stages are not numerous.

Classification. The class Basidiomycetes is subdivided into two sub-classes, the Heterobasidiomycetidae and the Homobasidiomycetidae. In the former the basidium is either septate or deeply divided, or may consist of a thick-walled resting spore called a **teleutospore** (Gr. *teleutaios* = last + *sporos* = seed, spore) which gives rise to a short tube on which the basidiospores are borne. In the Homobasidiomycetidae the basidium is simple, conforming to the type described on page 432.

KEY TO THE SUB-CLASSES OF THE CLASS BASIDIOMYCETES

- | | |
|---|-------------------------------|
| A. Basidium septate or deeply divided, or consisting of a teleutospore germinating into a promycelium; basidiospores usually capable of germinating by repetition | <i>Heterobasidiomycetidae</i> |
| AA. Basidium not septate or deeply divided; basidiospores usually germinating by germ tube | <i>Homobasidiomycetidae</i> |

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20 sub-class HETEROBASIDIO- MYCETIDAE jelly fungi, rusts, and smuts

Introduction. The Heterobasidiomycetidae are the jelly fungi, the rusts, and the smuts. The mature basidium in the sub-class typically consists of two portions: a basal **hypobasidium** (pl. **hypobasidia**; Gr. *hypo* = under + *basidium*) and an elongated tube or inflated protuberance, the **epibasidium** (pl. **epibasidia**; Gr. *epi* = upon + *basidium*), which typically bears basidiospores on sterigmata. In many species the hypobasidium produces two or more epibasidia. Many basidiospores are capable of producing on germination a secondary basidiospore which is shot off in the same manner as was the original spore (germination by repetition).

The basidium begins its development as a binucleate hyphal cell, the **probasidium** (pl. **probasidia**; Gr. *pro* = before + *basidium*) which may undergo a number of morphological changes before it becomes differentiated into a mature basidium. In some groups the probasidium becomes encysted with a thick wall and behaves as a resting spore. The probasidium eventually becomes transformed into the hypobasidium, which gives rise to the epibasidium, so that, in general, the terms probasidium and hypobasidium refer to early and late stages, respectively, in the development of the same basal basidial structure. The character of the probasidium is of considerable importance in phylogenetic considerations. Unfortunately, the terminology of the basidium and its parts has not been standardized in mycological literature. The terminology I am adopting is that of Rogers (1934) and Martin (1957). For other usage see Donk (1954, 1956), Linder (1940), and Talbot (1954). A comparative, illustrated terminology is given by Ainsworth (1961, p. 49).

Mycologists disagree somewhat on the classification of this sub-

class into orders and families. We shall adopt Martin's (1961) classification and place these fungi into three orders: Tremellales, Uredinales, and Ustilaginales. We shall also discuss briefly an interesting family of fungi, the Sporobolomycetaceae, sometimes classified with the imperfect yeasts (Lodder *et al.*, 1958) but without doubt belonging to the Basidiomycetes (Martin, 1945; Laffin and Cutter, 1959).

SIMPLE KEY TO THE ORDERS OF THE SUB-CLASS HETEROBASIDIOMYCETIDAE

- A. Basidiocarp usually well developed;
mostly saprobic, some species para-
sitic on plants or scale insects *Tremellales*
- AA. Basidiocarp lacking or poorly de-
veloped; mostly parasitic on vascu-
lar plants
 - B. Teleutospores present; plant
parasites
 - C. Basidiospores produced
on sterigmata; forcibly
discharged *Uredinales*
 - CC. Basidiospores sessile; not
forcibly discharged *Ustilaginales*
 - BB. Teleutospores lacking; resting
spores may be present; saprobic Family *Sporobolomycetaceae*¹

¹ A family of Basidiomycetes of uncertain affinity which cannot be included at present in any of the existing orders.

THE JELLY FUNGI

Introduction. The jelly fungi are Basidiomycetes whose fruiting bodies often have the consistency of jelly. However, many species which belong to this group produce fruiting bodies which are waxy or even cartilaginous. Of little economic importance as a whole, the group nevertheless contains a few species which are connected with destructively parasitic mycelia, and some others which show promise for use in the commercial production of carotenoids.

General Characteristics. The primary mycelium of the jelly fungi generally originates from a uninucleate basidiospore, conidium, or oidium. Conidia often bud off from the basidiospores; oidia are formed by fragmentation of the primary or secondary mycelium and

are therefore uninucleate or binucleate, respectively. Conidia and oidia germinate to give rise to monokaryotic or dikaryotic mycelium as the case may be. The secondary binucleate mycelium usually originates from the primary mycelium, presumably after sexual reproduction, which in some species at least takes place by the fusion of two compatible hyphae (Barnett, 1937). Dikaryotization having taken place in some such manner, the binucleate mycelium, which may or may not possess clamp connections, proceeds to form fruiting bodies and basidia of various types characteristic of the fungi which bear them.

Classification. Martin (1961) places all the jelly fungi in the order Tremellales, which he subdivides into nine families as follows:

order TREMELLALES

- Family Ceratobasidiaceae
- Family Tulasnellaceae
- Family Sirobasidiaceae
- Family Dacrymycetaceae
- Family Tremellaceae
- Family Hyaloriaceae
- Family Phleogenaceae
- Family Auriculariaceae
- Family Septobasidiaceae

You will find a good key to these families in Martin's *Revision of the North Central Tremellales* (1952).

Only a few of the above families will be discussed, but if you are interested in the various points of view on the classification and phylogeny of these fungi, you should refer to Rogers (1933), Linder (1940), Martin (1945, 1952), Bessey (1950), Gäumann (1952), Donk (1954, 1956), and Olive (1957).

family CERATOBASIDIACEAE

This small family of jelly fungi appears to be of considerable importance in determining phylogenetic relationships not only among the Heterobasidiomycetidae but also between them and the Homobasidiomycetidae. *Ceratobasidium*, the typical genus, has a somewhat inflated *aseptate* hypobasidium, which begins as an almost spherical probasidium and later develops epibasidia which tend to be long and inflated, not unlike the sterigmata of some primitive Homobasidiomycetidae. On the other side of the fence, so to speak, we

have *Metabourdotia*, in which the basidium is *longitudinally septate, but only part way to the base*. In the Tremellaceae, as we shall see presently, the basidia are *longitudinally septate all the way*. Thus, according to this interpretation, a *Ceratobasidium*-like ancestor may have given rise on one side to the line which leads to the Homobasidiomycetidae, and on the other to the line which leads to the Tremellaceae and beyond. For another interpretation, see Olive (1957). The fact is that there is an almost complete series of intermediate forms on both sides of *Ceratobasidium*. The problem is to interpret the direction of evolution.

family DACRYMYCETACEAE

The Dacrymycetaceae are jelly fungi whose fruiting bodies you can easily recognize in the field as small bodies, often bright yellow or orange, jelly-like or waxy, which you will find on the branches or trunks of living or dead trees. You can find them almost any time of the year during wet weather, but possibly more frequently in the fall, winter, and early spring.

The major pigment responsible for the yellow or orange color characteristic of these fungi is beta-carotene (Hanna and Bulat, 1953). Pigment formation is dependent on light, but once the pigment is formed it remains stable even after the organism is subjected to continuous darkness for 10 days (Bulat, 1954).

The chief characteristic which distinguishes members of this family from other Basidiomycetes is the character of the basidium. The hypobasidium, borne terminally on a binucleate hypha, is elongated and somewhat thicker than the parent hypha. At the tip, it produces two long arms, the epibasidia, each of which terminates into a pointed sterigma on which a sausage-shaped basidiospore is obliquely perched. We call this type of basidium the "tuning fork" type.

The Dacrymycetaceae produce various types of basidiocarps. *Cerinomyces*, for example, produces flat, crust-like, waxy fruiting bodies; in *Dacrymyces* the basidiocarps are gelatinous in texture and cushion-shaped, with a smooth or wrinkled surface; in *Calocera* (Figure 152) the fruiting bodies are long and tapering, often branched, and waxy; in *Ditiola* they consist of a stalk and head, the latter pitted, ridged, or wrinkled, superficially resembling a miniature morel.

The life histories of most species have not been worked out in detail. *Dacrymyces deliquescens* (Figure 153) is the best-known species. The elongated, curved, uninucleate basidiospores of this spe-



Figure 152. *Calocera cornea*. Photograph by Fred W. Kent.

cies usually become three-septate at the time of germination (Figure 153H). One or more minute conidia (Figures 153K, L) now bud from each cell of the basidiospore and then germinate by a germ tube which develops into the mycelium. Sometimes, instead of producing conidia, the basidiospores give rise to germ tubes directly (Figure 153I). The mycelium thus produced, from either the conidia or basidiospores, is uninucleate (Figure 153J).

We do not know how dikaryotization takes place in the Dacrymycetaceae, but we find that the fruiting bodies are formed only by the binucleate mycelium (Figures 153A, B). Yen (1949) found *Calocera cornea* to be tetrapolar heterothallic. He also reported *Dacrymyces deliquescens* as heterothallic but reached no conclusion about its type of heterothallism (bipolar or tetrapolar). The basidiocarps of these fungi are orange in color when young but change to yellow with age. They vary from 1 to about 6 millimeters in diameter, but often coalesce and form large masses. The fruiting bodies are soft and gelatinous in texture. They are composed of dikaryotic hyphae of small diameter which are completely surrounded by jelly.

When the fruiting body has reached a certain stage of maturity, the hyphae on the periphery begin cutting off a large number of binucleate oidia (Figure 153C). These accumulate on the jelly-like

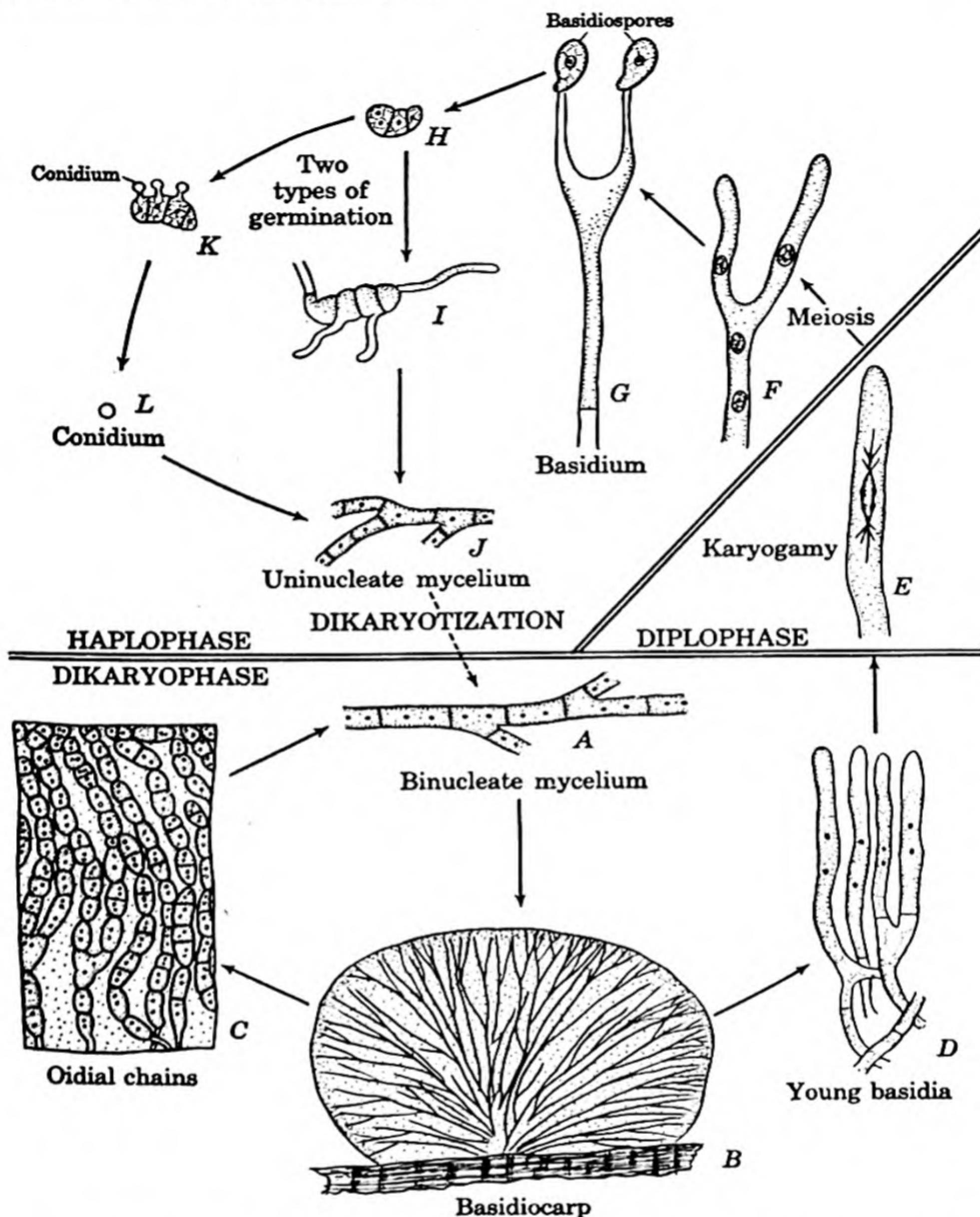


Figure 153. Life cycle of *Dacrymyces deliquescentis*. A, D, G, H, K, L, redrawn from Dangeard, 1895, *Botaniste*, 4:119–181; B, C, redrawn by permission, from *Researches on fungi*, Vol. 2, by A. H. R. Buller, copyright 1922, Longmans, Green and Company, London; E, F, redrawn from Juel, 1898, *Jahrb. wissen. Bot.*, 32:361–388; I, redrawn by permission from *Fungi*, by M. C. Cooke and M. J. Berkeley, 1888, D. Appleton & Co., New York.

surface of the basidiocarp and, when the sporophore is wet, slide down the jelly. They are thus disseminated by water as it runs off. The oidia germinate easily and produce binucleate mycelium (Yen, 1949).

As the perennial sporophores become older, production of basidia begins. These are formed side by side in the basidiocarp from the tips of the binucleate hyphae, forming a hymenial layer. At first, the young basidia are binucleate and club-shaped (Figure 153D). Karyogamy then occurs, and as meiosis is taking place the tip of the young hypobasidium branches to form two epibasidia (Figures 153E-F) which push through the jelly to the surface and form the tuning fork. Two of the four haploid nuclei formed by meiosis now migrate one into each epibasidium and through the sterigmata into the basidiospores (Figure 153G). The other two nuclei remain in the hypobasidium and eventually disintegrate. The mature basidiospores are shot off the basidium. For an excellent step-by-step description of basidiospore discharge in *Calocera* (Figure 150) read Buller's account (1922).

Bulat (1953) found that colonies of *Dacrymyces ellisii* growing in agar culture produce no basidia but form four types of asexual spores: oidia, chlamydospores, ellipsoidal spores borne in clusters (conidia?), and ballistospores. This last type is of particular interest because it gives further evidence of the possible affinity of the Sporobolomycetaceae (page 453) to the Tremellales.

For a taxonomic treatment of the Dacrymycetaceae see Martin (1952) and Kennedy (1958a, b).

family TREMELLACEAE

As in the Dacrymycetaceae, the basidiocarps of the Tremellaceae vary from crust-like to stalked. In some forms the basidiocarp is but a thin layer of gelatinous hyphae which produce the basidia. In some species of *Exidia* and *Tremella*, the most common genera in this family, the basidiocarps are shaped like cushions but have a highly wrinkled surface. They are gray, purplish, or brown. The fruiting body of *Tremella fuciformis*, on the other hand, is pure white. It consists of a number of rather large, leaf-like folds on which the hymenium is formed. Some species of *Tremella* are used extensively as food by the Chinese people. In some of the higher Tremellaceae, the basidiocarps are rather large and complex. In *Phlogiotis* (Figure 154) the fruiting bodies reach a height of 3 or 4 inches; they are pink or orange-red, and have the shape of one-half of a funnel. They bear



Figure 154. *Phlogiotis helvelloides*. Photograph by Philip G. Coleman.

their basidia on the outer surface of the funnel. Tooth-like protuberances lined with hymenium cover the lower surface of the large sporophore of *Pseudohydnum*. Finally, *Tremellodendron* may produce a many-branched sporophore which attains considerable size.

Life Cycle. *Exidia glandulosa*, a common species of the Tremellaceae, will serve as our example of a general life history. The young basidiocarps are composed of more or less uniform, thin, binucleate hyphae which bear clamp connections (Figure 155C). The first sign of basidial formation is the swelling of the tips of certain hyphae just below the surface of the jelly enveloping the basidiocarp. The structure which develops is the young basidium, which is binucleate at first but soon becomes uninucleate by the fusion of its two nuclei (Figures 155E, F). Meiosis follows karyogamy (Figure 155G). After the first division of the zygote nucleus a vertical septum is

formed which divides the hypobasidium into two halves (Figures 155H, I). After the second nuclear division, two more septa, at right angles to the first, divide the hypobasidium into four uninucleate quarters. In the meantime a basal septum forms and separates the

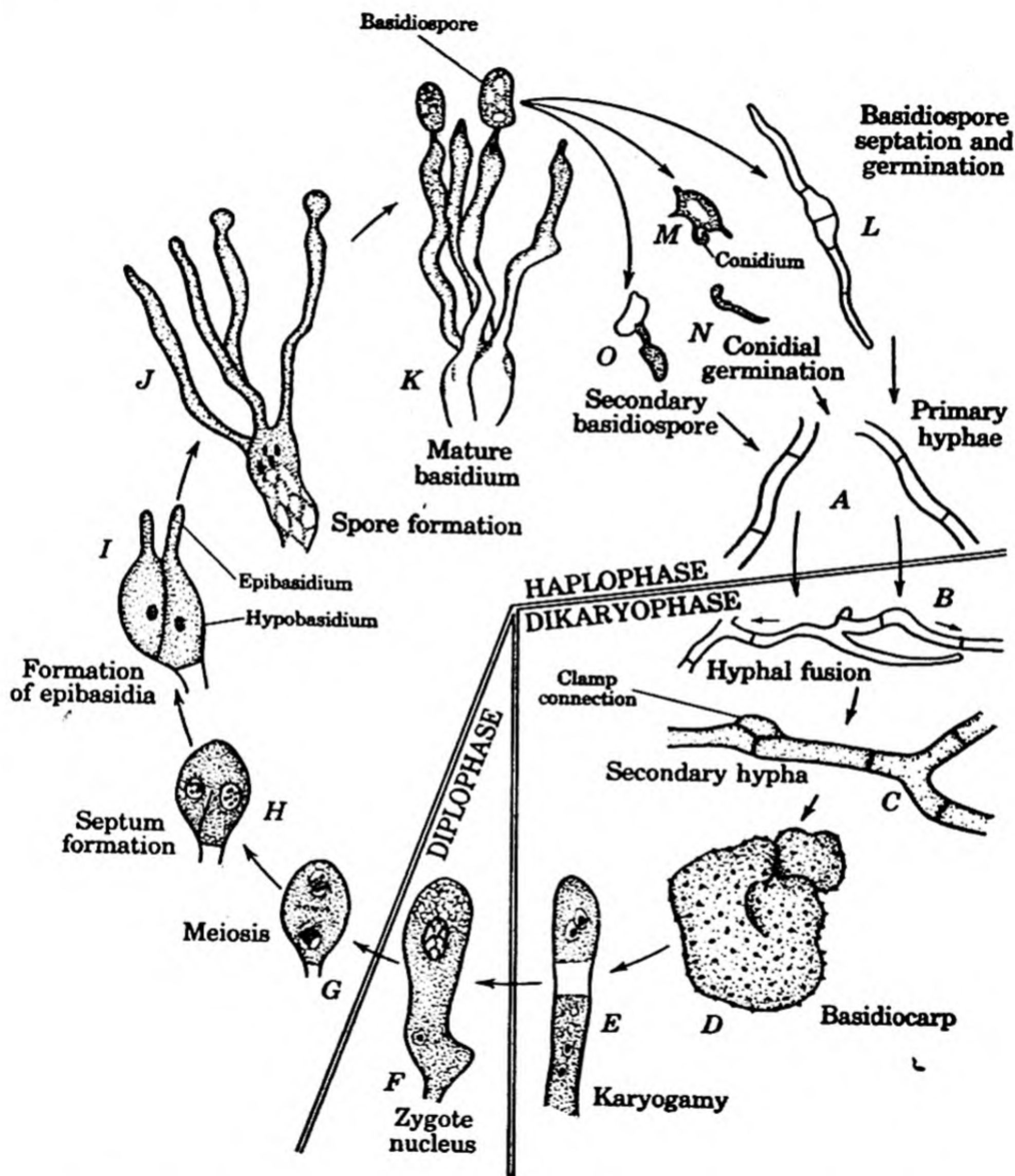


Figure 155. Life cycle of *Exidia glandulosa*. A, B, L-O, redrawn from Barnett, 1937, *Mycologia*, 29:626-649; D, redrawn by permission from *Handbook of Australian fungi*, by M. C. Cooke, 1892, Williams and Norgate, London; E-K, redrawn from Whelden, 1935, *Mycologia*, 27:41-57.

basidium from the parent hypha. Each basidial cell now produces an epibasidium which pushes through the jelly to the surface and ends in a pointed sterigma on which a curved basidiospore develops (Figures 155J, K). The nuclei in the septate portion of the hypobasidium then migrate into the basidiospores. The latter are violently discharged into the air and are distributed by air currents.

Basidiospores of *Exidia glandulosa* germinate in one of three ways: (1) one or two germ tubes issue from the basidiospore and grow into mycelium (Figure 155L); (2) several slender, short germ tubes issue from the basidiospore, each bearing a tiny, curved conidium which falls off, germinates, and forms mycelium (Figures 155M, N); (3) the basidiospore produces a short, pointed sterigma which produces a secondary basidiospore similar to the primary one. Septation of the basidiospore occurs generally at the time of germination (Figure 155O).

Basidiocarps (Figure 155D) arise normally from secondary mycelium. Such mycelium originates by the fusion of primary hyphae and exhibits clamp connections (Figures 155B, C). Dikaryotization apparently takes place in this manner. I have based the above account of the life history of *Exidia glandulosa* on the papers by Whelden (1935) and Barnett (1937).

family AURICULARIACEAE

The Auriculariaceae is a rather large family which includes thirteen genera of jelly fungi (Martin, 1952). The distinguishing feature of this family is the transversely or obliquely septate basidium, which may or may not be differentiated into a hypobasidium and an epibasidium. In a few species the probasidium develops into a cyst whose walls, however, are not greatly thickened.

The fruiting bodies of the Auriculariaceae vary from a simple weft of hyphae, as in *Helicobasidium*, to the well-developed, large, fruiting body of *Auricularia*, which is gelatinous and somewhat leathery (Figure 156C).

Most of these fungi are saprobic, but *Eocronartium muscicola* and *Jola javanensis* are parasitic on mosses, and *Helicobasidium purpureum* on the roots of some flowering plants. A few other species are also known to parasitize plants; among them is *Herpobasidium deformans*, which causes a blight of honeysuckle leaves (Gould, 1945).

Auricularia auricula, which is probably the most common and most widely distributed of the Auriculariaceae, produces the largest

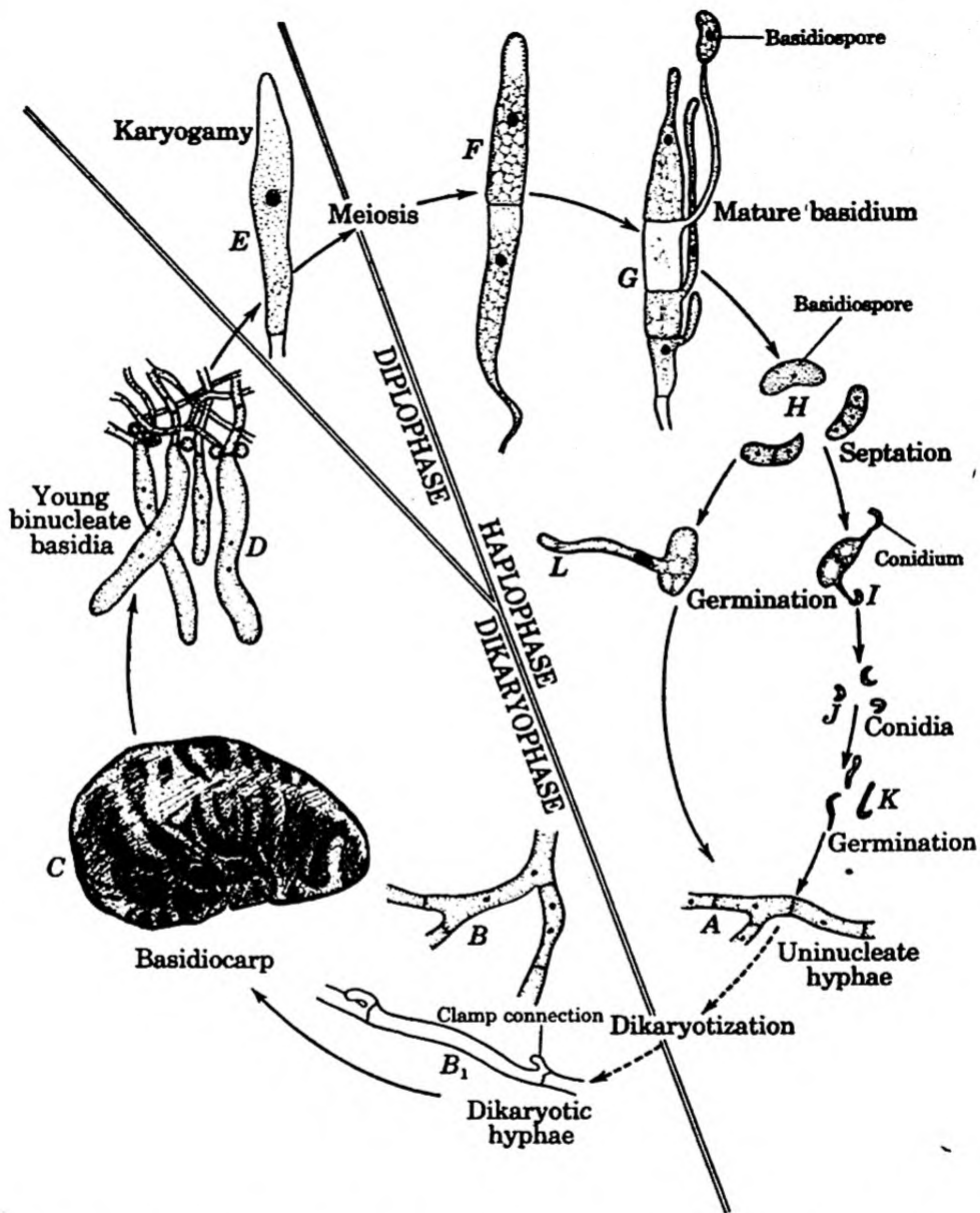


Figure 156. Life cycle of *Auricularia auricula*. A, constructed; B, D–G, L, redrawn from Sappin-Trouffy, 1896, *Botaniste*, 5:44–58; B₁, H–K, redrawn from Barnett, 1937, *Mycologia*, 29:626–649; C, drawn by permission from photograph by Peck in *Researches on fungi*, Vol. 2, by A. H. R. Buller, 1922, Longmans, Green and Company, London.

fruiting body of any member of this family. This is an ear-shaped, gelatinous structure (Figure 156C) which consists of binucleate hyphae bearing clamp connections. The hymenium is formed on the underside, a large number of hyphal ends developing into basidia. At first binucleate, the young basidia become uninucleate by karyogamy. The zygote nucleus eventually undergoes meiosis, and the elongated basidium becomes four-celled by the development of three transverse septa. One septum forms after the first nuclear division, and the other two form after the second.

A long arm (epibasidium) now grows out from each cell, and turns in the same direction toward which the hypobasidium is pointing. Growth continues until the arms protrude above the surface of the jelly which envelops the entire basidiocarp. A curved basidiospore now develops on a sterigma at the tip of each of these arms, and the basidial nuclei migrate into the basidiospores (Figures 156D–G).

The basidiospores of *Auricularia auricula* become multiseptate at the time of germination and germinate in the same way as those of *Exidia glandulosa*, described in the discussion of the Tremellaceae (Figures 156H–L). Barnett (1937) has observed the fusion of hyphae issuing from basidiospores and the production of clamp connections in presumably dikaryotic hyphae which have originated in this way (Figure 156B). *Auricularia auricula* is one of the fungi in which the dolipore septum was discovered by Moore and McAlear (1962).

family SEPTOBASIDIACEAE

This is a family of about 160 species which includes the genera *Septobasidium* and *Uredinella*. Both are parasitic on scale insects. Members of this family resemble the Auriculariaceae in that they produce transversely septate basidia. They differ from most Auriculariaceae in that the fruiting bodies of the Septobasidiaceae are not gelatinous. They differ also in their biology, the Auriculariaceae being saprobic or parasitic on plants, whereas the Septobasidiaceae are parasitic on insects. Of evolutionary significance is the fact that in most species of *Septobasidium* the wall of the probasidium is often thick and the whole structure resembles a spore. The probasidium eventually puts out an elongated epibasidium which soon becomes transversely septate into four cells. Each of these cells then produces a sterigma which in turn forms a basidiospore (Figure 157B). Such hypobasidia certainly appear to be similar to the teleutospores of the rusts (Uredinales), as you will see in another section (page 457) of this chapter.

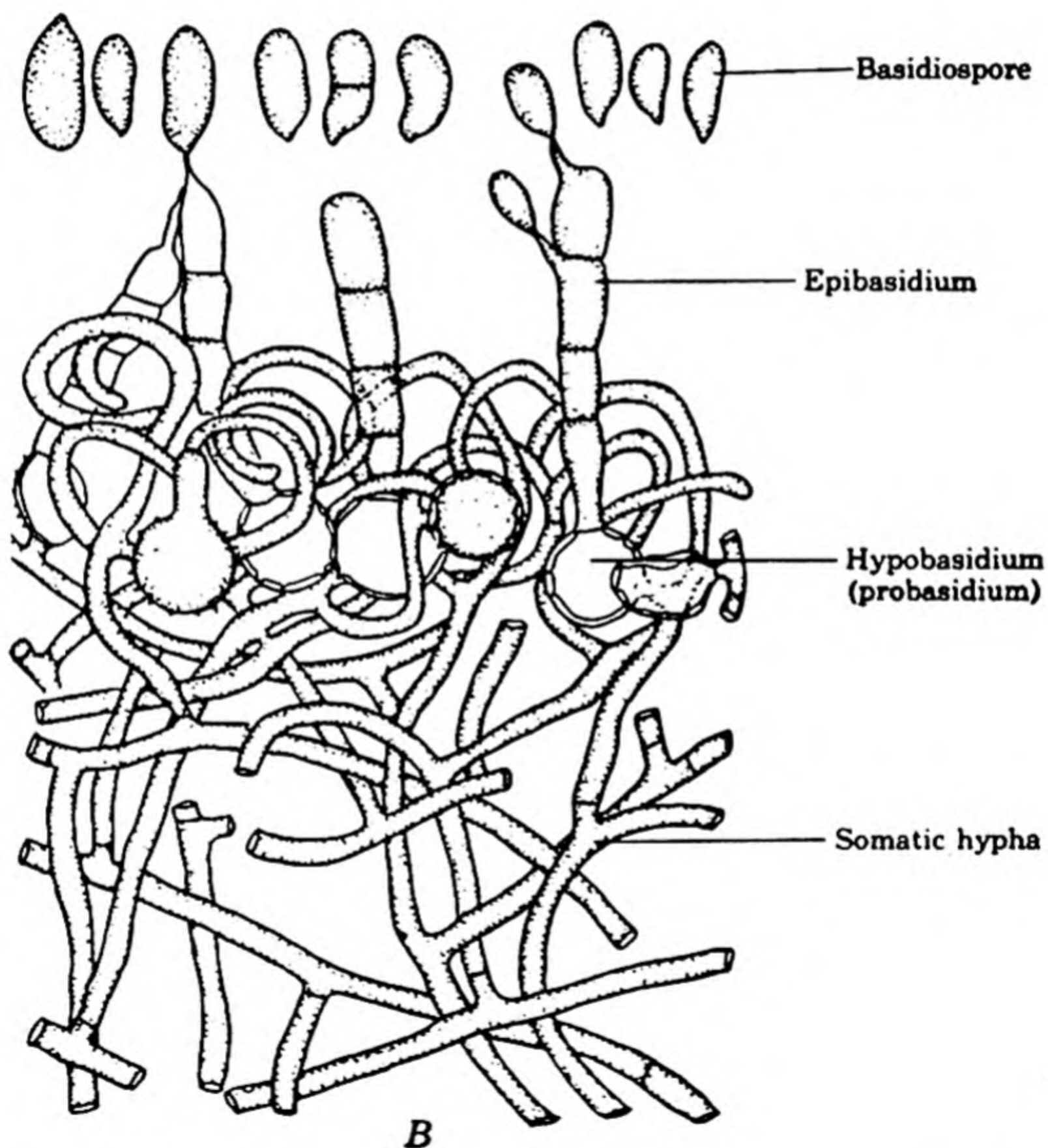
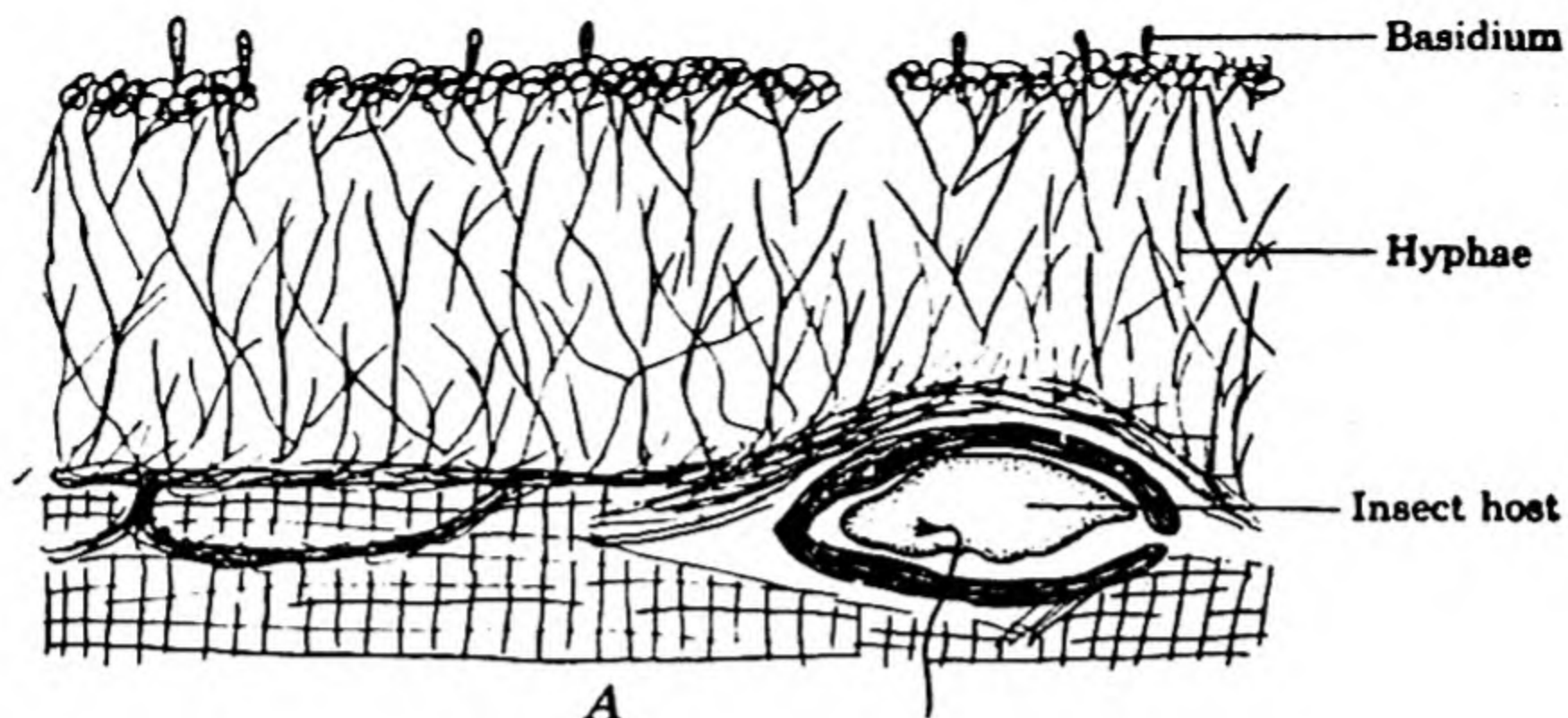


Figure 157. *Septobasidium fumigatum*. Redrawn by permission from *The genus Septobasidium*, by John N. Couch, 1938, University of North Carolina Press, Chapel Hill.

The genus *Uredinella* which, in addition to teleutospores, forms yet another type of binucleate spore, probably represents a link between the Septobasidiaceae and the rusts (Uredinales).¹ Couch, who discovered this genus, calls these spores uredospores, applying to them the same term as is used for the binucleate repeating spores (conidia) of the rusts. Unfortunately, Couch (1937) was unable to germinate the uredospores of *Uredinella*, and we do not know, therefore, what their subsequent development is. This discussion perhaps has little meaning to you at this point, but it should become clearer after you have studied the rusts and have become familiar with the role that teleutospores and uredospores play in their life cycle. These spores are particularly characteristic of the rusts, and therefore it is interesting to find them in some of the Septobasidiaceae.

The Septobasidiaceae are of interest biologically because of their relationship with their insect hosts. As mentioned above, all species in this family are parasitic on scale insects. The basidiospores germinate on the insect and send their hyphae into its body. As the insect attaches itself to its plant host, the fungus grows and forms a hyphal mat over the insect. These perennial hyphal mats generally build up intricate structures (Figure 157A) under which a colony of insects lives. The parasitized insects are not killed, but they are rendered sterile. *Septobasidium* parasitizes a whole colony of scale insects, whereas *Uredinella* confines its activities to single insects.

family SPOROBOLOMYCETACEAE

The Sporobolomycetaceae is a small family of simplified, yeast-like fungi which produce conidia on sterigmata and discharge them violently as ballistospores. Some species produce no mycelium, remaining unicellular and yeast-like throughout their life cycles. Other species, however, produce hyphae which consist of binucleate cells and bear clamp connections. Some of these characters of the Sporobolomycetaceae point convincingly to a basidiomycetous relationship.

The family includes five genera: *Sporobolomyces*, *Bullera*, *Sporidibolus*, *Itersonilia*, and *Tilletiopsis*. The first two remain yeast-like throughout their life cycles. The other three produce mycelium, at least under certain conditions.

Laffin and Cutter (1959), in a study of the life cycle of *Sporidibolus johnsonii*, report that the ballistospores are uninucleate and diploid (Figure 158A) and that they multiply, either by budding,

¹ See, however, Boedijn (1959), who presents a different point of view.

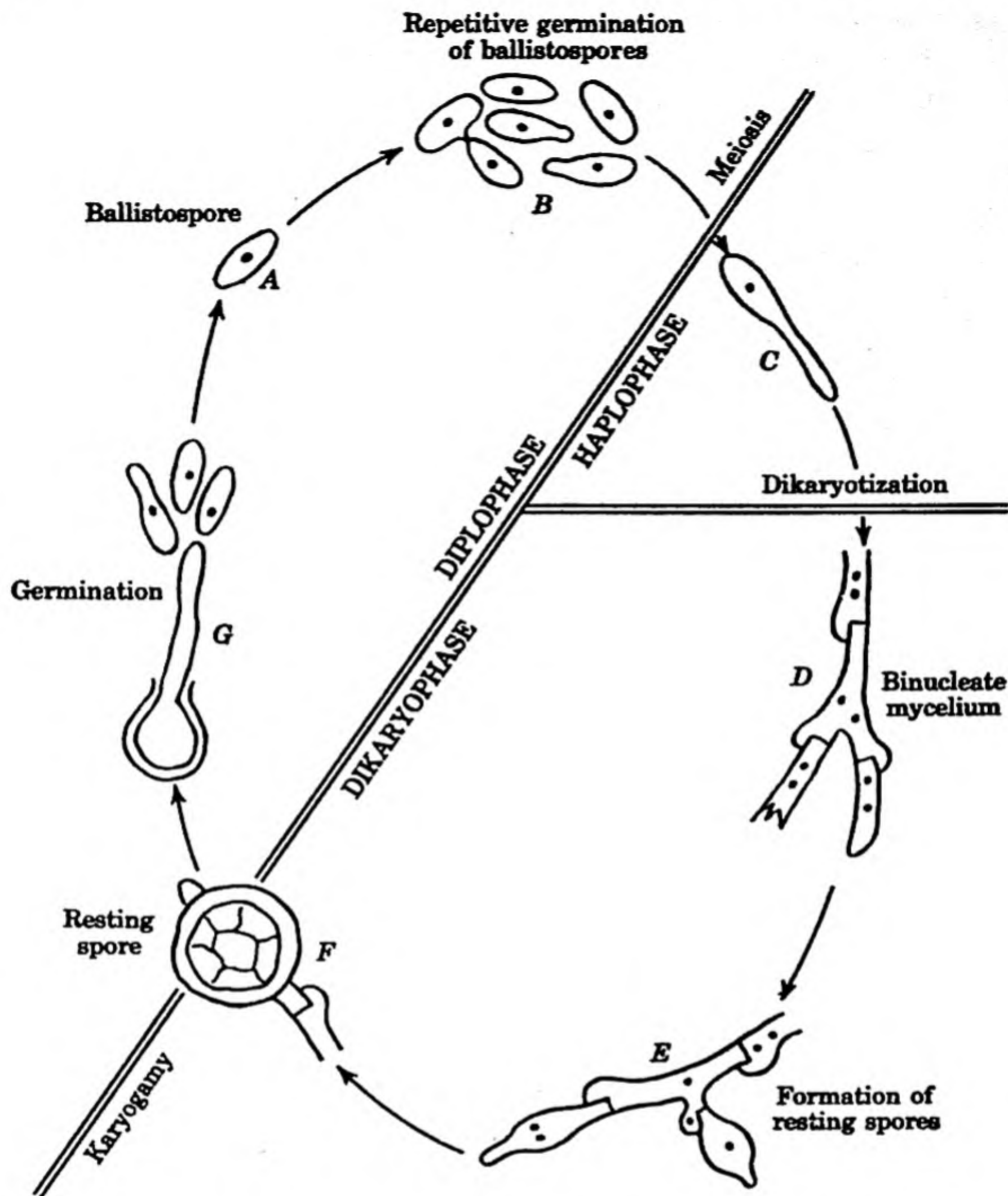


Figure 158. Life cycle of *Sporidiobolus johnsonii*. Redrawn from Laffin and Cutter, 1959, Jr. *El. Mitchell Sci. Soc.*, 75:89-96.

as yeasts do, or by repetition, producing new ballistospores on sterigmata (Figure 158B). It appears that, eventually, meiosis occurs in some ballistospores, rendering them quadrinucleate. After meiosis, such spores germinate, producing a binucleate mycelium with clamp connections (Figure 158D). Thus, no uninucleate, haploid mycelium is formed and no plasmogamy takes place. Short branches, which grow out of the binucleate mycelium, form resting spores in which karyogamy occurs (Figures 158E, F). Upon germination, the

resting spore produces a short germ tube from which uninucleate, diploid ballistospores are thrown off successively (Figure 158G). Although Laffin and Cutter were unable to make chromosome counts, they have presented strong evidence in support of this proposed life cycle.

Thus, if this life cycle is correct, we have, in *Sporidiobolus johnsonii*, a basidiomycete in which the diploid phase alternates with a dikaryotic phase, the two being of equal importance in the life cycle of the organism. Uninucleate, haploid spores are not formed. What structure or group of structures may be homologized with the basidium is an interesting question which I shall not attempt to answer.

Itersonilia perplexans produces both uninucleate and binucleate mycelium (Sowell and Korf, 1960/1962) each perpetuated by the production, release, germination, and growth of uninucleate or binucleate conidia and ballistospores, respectively.

The dikaryotic mycelium bears clamp connections and produces chlamydospores, in addition to the other structures. No plasmogamy, karyogamy, or meiosis has been discovered, and all attempts to derive the binucleate mycelium from the uninucleate or vice versa have failed.

Sowell and Korf (1960/1962) are inclined to believe that *Itersonilia*, *Sporidiobolus*, and *Tilletiopsis* should be considered one and the same organism. According to Cutter (Laffin and Cutter, 1959), *Sporobolomyces* and *Tilletiopsis* both exhibit complete sexual and asexual cycles, but these studies have not been published.

THE RUSTS

order UREDINALES

Occurrence, and Importance to Man. The Uredinales, or rusts, are among the most important of the Basidiomycetes economically. They are parasitic on plants and cause great losses to many cultivated crops. I need only mention black stem-rust of cereals, and white-pine blister rust, two diseases which have caused enormous damage, to emphasize the economic importance of these fungi. Other serious plant rusts, against which growers in different parts of the world have been fighting, include coffee rust, asparagus rust, bean rust, juniper rust, snapdragon rust, carnation rust, and scores of others. Many of these fungi, such as cereal rust, occur universally wherever a susceptible host grows, and the plant diseases

caused have been recognized since ancient times. Indeed, the ancient Romans considered the cereal rust diseases so important that they believed two gods, *Robigus* and *Robigo*, to be responsible for the rust, and planned annual festivals, the *Robigalia*, to propitiate these gods. Whether the Romans actually believed that the rust could thus be prevented or whether they used this "reasoning" as an excuse for yet another festival will always remain open to question.

General Characteristics. The mycelium of the rusts is uninucleate in its first phase and binucleate in its later stages. It grows intercellularly for the most part, obtaining its nourishment from the host cells by means of haustoria. At least this is the current belief concerning the function of haustoria. As in the downy mildews and the powdery mildews, here, too, haustoria originate in the intercellular hyphae and penetrate the cell walls against which the hyphae are growing. Production of haustoria appears to be a response of the hyphae to a contact stimulus and possibly to a chemical stimulus (Dickinson, 1949).

Hauustoria vary considerably in shape, size, and structure (Moss, 1926; Hunter, 1948). Sheathed haustoria have been known for many years, but the nature of the sheath is not clear. Ehrlich and Ehrlich (1961) report that in *Puccinia graminis tritici* the electron microscope shows a sheath of what may be naked protoplasm on the outside of the haustorial membrane in the invaded host cell. They interpret this to mean that haustorial protoplasm probably oozes out through ultra-microscopic pores in the wall and comes in intimate contact with the protoplasm of the host cell (Figure 159).

Clamp connections have been found in the binucleate mycelium of a few species of rusts, but, in accordance with present information, they seem to be infrequent and to be confined only to certain regions of the mycelium.

Up to 1951, no one had succeeded in growing any of the Uredinales on artificial media, and the rust fungi were considered to be obligate parasites. In that year Hotson and Cutter announced in a short paper that they had grown *Gymnosporangium juniperi-virginianae*, one of the rusts, on artificial media. In 1959 Cutter published a lengthy, detailed paper on his work with this fungus, stating that he had seven strains of this species growing in agar culture. In 1960 he announced that he had succeeded in growing *Puccinia malvacearum*, the causal organism of hollyhock rust, in axenic culture (Gr. *a* = not + *xenos* = stranger; i.e., without another organism being present). A later paper (Cutter, 1960/1961)

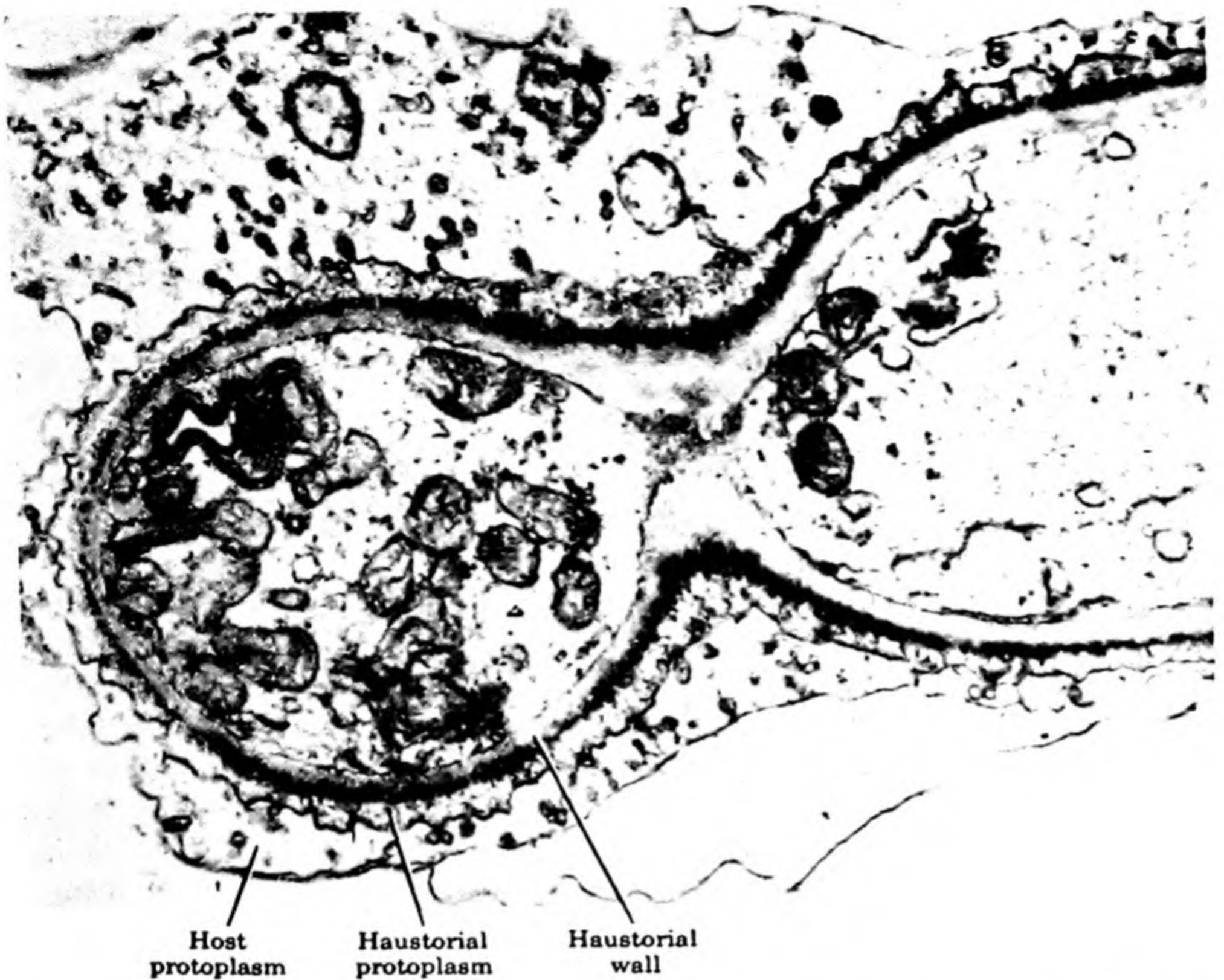


Figure 159. Electron micrograph of haustorium of *Puccinia graminis*. Courtesy Ehrlich and Ehrlich.

discusses the axenic culture of yet another species of rust, *Uromyces ari-triphylli*.

The rusts produce no basidiocarps. The basidial apparatus of the Uredinales differs considerably from that of most Heterobasidiomycetidae. The structure in which karyogamy takes place is a thick-walled teleutospore, not unlike that of some species of *Septobasidium*. The teleutospore originates at the tip of a binucleate hypha. Teleutospores are generally thick-walled and serve as resting spores. Most rusts overwinter in the teleutospore stage, but in some species the teleutospore germinates soon after it is formed.

A mature teleutospore may be unicellular or multicellular, depending on the species. When it is first formed each of its cells is binucleate. Karyogamy eventually takes place, however, and renders the teleutospore cells diploid and uninucleate. When favorable con-

ditions for germination arrive, a short germ tube, the promycelium, grows out from each cell. The diploid nucleus now migrates into the promycelium, undergoes meiosis, and produces four haploid nuclei which distribute themselves at more or less equal distances in the promycelium. The formation of three septa between the nuclei divides the promycelium into four uninucleate cells, each of which then produces a sterigma at the tip of which a basidiospore develops. The four nuclei in the promycelium now migrate into the basidiospores, and the latter are then forcibly discharged into the air by the water drop method characteristic of the Basidiomycetes.

Thus, the basidial apparatus of the rusts consists of (1) the teleutospore, which is an encysted probasidium developing into a hypobasidium upon germination, and (2) the promycelium, which is the epibasidium.

Life Cycle Pattern. All rusts except the so-called imperfect rusts (Uredinales Imperfecti; see page 466) produce teleutospores. Mycologists consider the teleutospores the perfect stage of the Uredinales, since it is in these structures that karyogamy and meiosis take place. Besides the teleutospores, most rusts produce other spores as well. As a matter of fact, the life cycle of a rust is typically very complex, consisting of four or five distinct reproductive stages. The Uredinales fall into two general life cycle patterns: (1) the long-cycled (macrocyclic) rusts and (2) the short-cycled (microcyclic) rusts. A long-cycled rust produces at least one type of binucleate spore in addition to the teleutospore. In short-cycled rusts, the teleutospores are the only binucleate spores produced.

Cummins (1959) further subdivides the macrocyclic pattern into macrocyclic and demicyclic, the former with four stages in addition to the basidiospores, the latter with two or three.

A typically long-cycled rust produces five distinct stages in a regular sequence. These are as follows:

Stage 0	Spermogonia bearing spermatia and receptive hyphae.
Stage I	Aecia bearing aeciospores.
Stage II	Uredia bearing uredospores.
Stage III	Telia bearing teleutospores.
Stage IV	Promycelia bearing basidiospores.

We shall discuss each of these stages separately before we try to fit them into a specific life cycle pattern.

Spermogonia and Receptive Hyphae. The spermogonia (also called pycnia; sing. pycnium) are the structures which bear the sex organs of the Uredinales. The spermatia are the male sex organs,

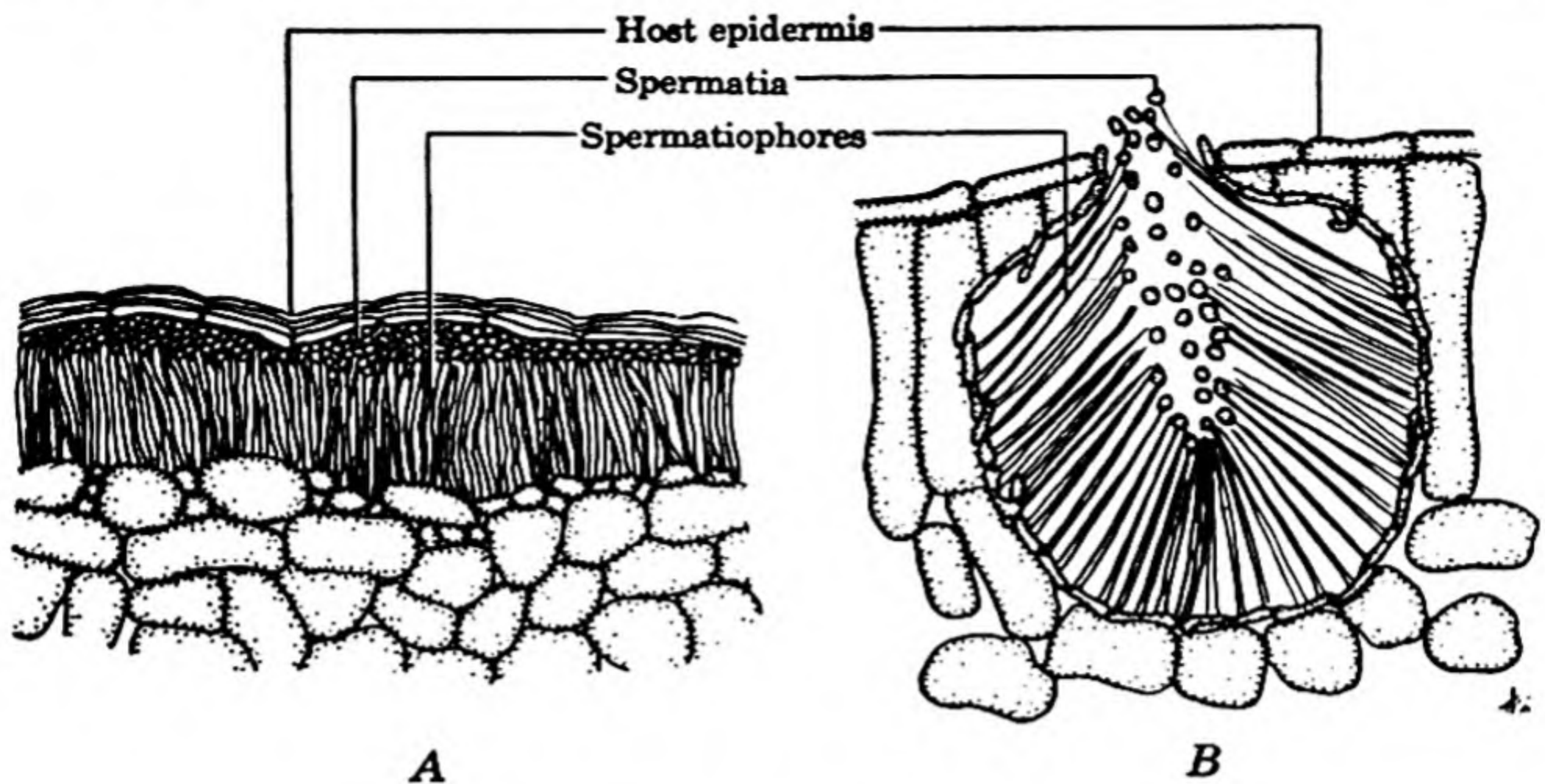


Figure 160. Two types of rust spermogonia.

and the receptive hyphae are the female sex organs. The spermogonia are produced from primary, uninucleate mycelium growing in the tissues of the host. There are several types of spermogonia in the rusts.¹ Some are more or less globose or flask-shaped, but others are flat and sprawling (Figure 160). The former type, which is probably the more typical, develops as follows. About 4 days after infection of the host by a basidiospore has taken place, a thin stromatic mass of uninucleate hyphae develops below the epidermis of the host. From this mycelial mat a number of hyphal branches originate which converge toward a common point. The outer spermogonial wall soon becomes organized, and a cavity begins forming in the center. The wall cells now send into the cavity a great many closely packed, elongated, uninucleate spermatophores, each of which, by successive division of its nucleus, cuts off a series of uninucleate spermatia (also called pycniospores) from its tip. These spermatia, formed in chains, are released in enormous numbers in the spermogonial cavity. In the meantime, an ostiole has developed in the upper part of the flask-shaped spermogonium, and a number of slender threads—the periphyses—developed from the upper edge of the wall, converge toward a central point and curve upward. The tips of these periphyses, pushing against the host epidermis from below, rupture it and protrude above it through the opening they have created.

¹ At least nine types, according to Hiratsuka (1961).

The spermatia, which are cut off from the tips of the spermatophores, fill the spermogonial cavity and are exuded from the ostiole in a droplet of nectar, a thick, sticky, sweet liquid.

The receptive hyphae, which behave as the female organs of the fungus, are produced from the upper part of the spermogonial wall, arising just below or among the periphyses; they grow out through the ostiole into the drop of nectar; they are cylindrical with blunt tips, and flexuous. The periphyses of the spermogonia sometimes change into such flexuous hyphae by elongation, and then behave as receptive hyphae for spermatia, but, as we shall see in a later paragraph, spermatia and receptive hyphae (or periphyses behaving as receptive hyphae) produced by the same mycelium are not compatible.

In the old days, when mycologists did not know the function of "pycnia and pycniospores," they called the spermogonial stage stage 0. Although we now know the function of these structures, the old familiar designation of stage 0 is too well established to be changed.

Aecia and Aeciospores. Aecia and aeciospores form next in sequence in the rust life cycle. [Aecium (pl. aecia) comes from the Greek, *aikia*, which means injury, and refers to the blisters on the host resulting from the formation of aecia by the parasite.] An aecium is a group of binucleate hyphal cells within the parasitized host which give rise to spore chains by successive and conjugate divisions of the nuclei.

The basal cells of the aecium are the aeciospore mother cells. Uninucleate mycelium in the host forms the aecial primordium whose cells are, consequently, uninucleate at first. However, in some manner which is not clear, either these cells become binucleate, or new binucleate cells which have been formed as a result of spermatization (see discussion on page 470) appear among them. These binucleate cells (aeciospore mother cells) which form the basal layer in the aecial primordium begin to divide, producing alternately aeciospores and disjuncter cells. As the aeciospore mother cells divide, their nuclei divide conjugately, two daughter nuclei remaining in the aeciospore mother cell while the other two go into the daughter cell, which alternately differentiates into an aeciospore or a disjuncter cell. Closely packed parallel chains of cells are thus formed, with the oldest cells at the tip of the chain and the youngest adjacent to the aeciospore mother cells at the aecial base.

In most species of rusts the peripheral cells of the aecial base give rise by successive division to a wall which surrounds the spore chains

in the form of a cup. This wall is the peridium. In a young aecium which has not broken through the host epidermis, the peridium surrounds the spore chains on all sides, forming a complete dome over them. When the aecium matures, the spore chains push through the roof of the peridium and the spores are liberated. The torn peridium forms a lip around the edge of the aecial cup.

The peridial lip of the mature aecium is short in some species, long and shredded in others, and large, irregular, and flaring in still another group of rusts. In some species no peridium is formed, the aecium being confined to the basal sporogenous cells (Figure 161).

As the aecium develops, the disjuncter cells disintegrate and the spores thus separate from each other. When aecia are produced in a leaf, they are generally located in the lower portion and break through the lower epidermis.

Uredia and Uredospores. Uredospores, which constitute the repeating stage of the rusts, are borne in structures which resemble acervuli and which we call **uredia** (sing. **uredium**; L. *urere* = to burn), because of their reddish color. The uredial cells are formed from binucleate mycelium originating from the germination of an aeciospore or a uredospore. This mycelium produces the uredia subepidermally. As the uredospores form, they press against the host epidermis from the inside and rupture it, pushing it out in the same manner as the conidia from an acervulus in any of the Melanconiales. Uredospores are attached on long stalks. The spores themselves are generally globose or oval, with a fairly thick wall covered with minute spines. The uredospores appear colorless or straw-colored under the microscope, but they contain a dilute reddish pigment which you can see when you look at masses of uredospores on the host. Most uredia do not have a peridium, but some do. In the rust genus *Coleosporium*, the uredospores form chains, and it is difficult to distinguish them from aeciospores (Figure 162A).

From the standpoint of propagation of the fungus, the uredial stage is probably the most effective. Uredospores first form in the late spring and continue forming throughout the summer, spreading the fungus from plant to plant and from field to field. They are the summer spores of the rusts and are regarded as the conidia of these fungi, since they represent the only repeating stage. When a uredospore germinates, it produces a binucleate mycelium which, in a matter of a few days, forms new uredia and uredospores. Several generations of uredospores are therefore produced in a single season.

Telia and Teleutospores. Telia are groups of binucleate cells which produce teleutospores. These spores vary enormously in dif-

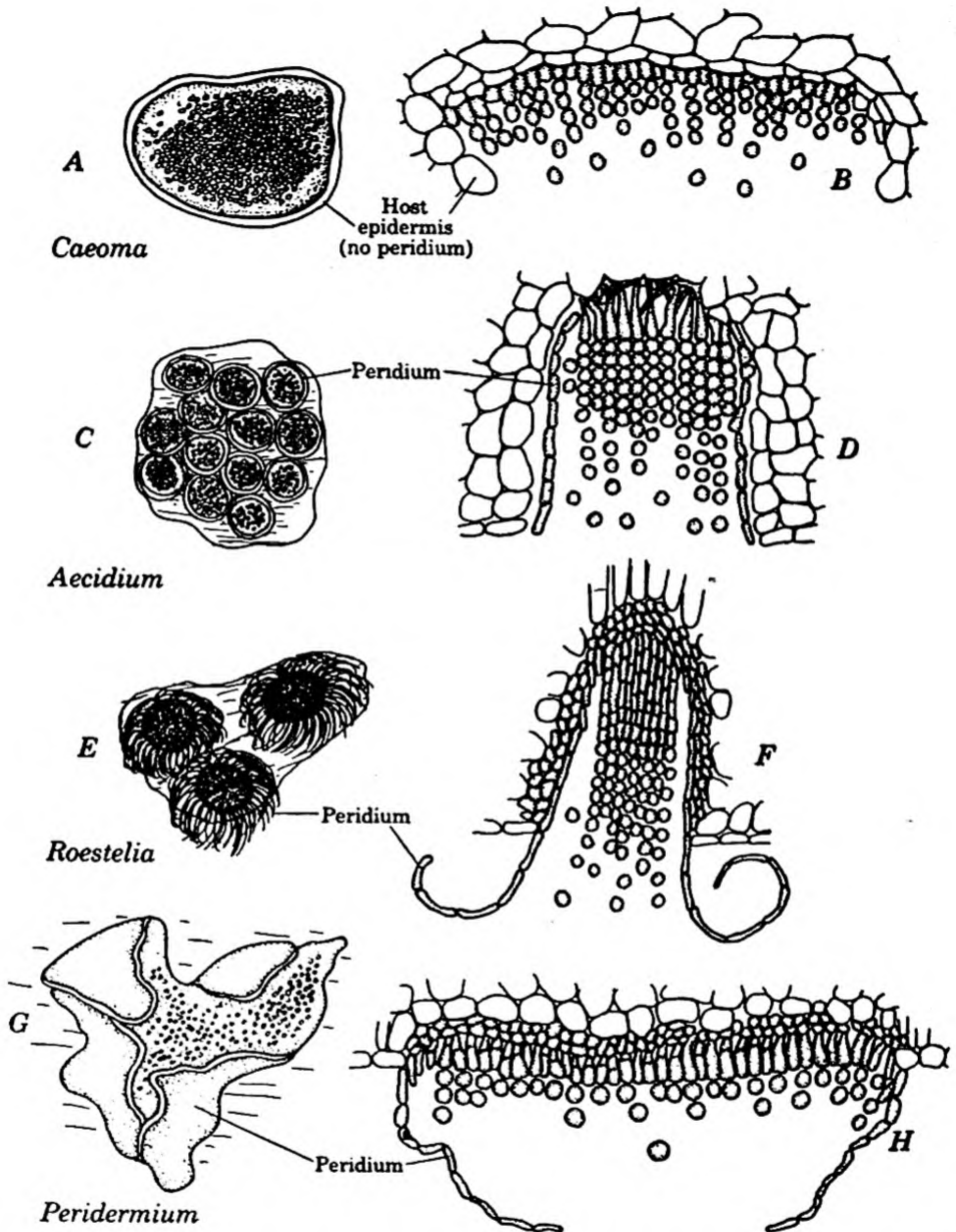


Figure 161. Four types of aecia illustrating the form-genera *Caeoma*, *Aecidium*, *Roestelia*, and *Peridermium*.

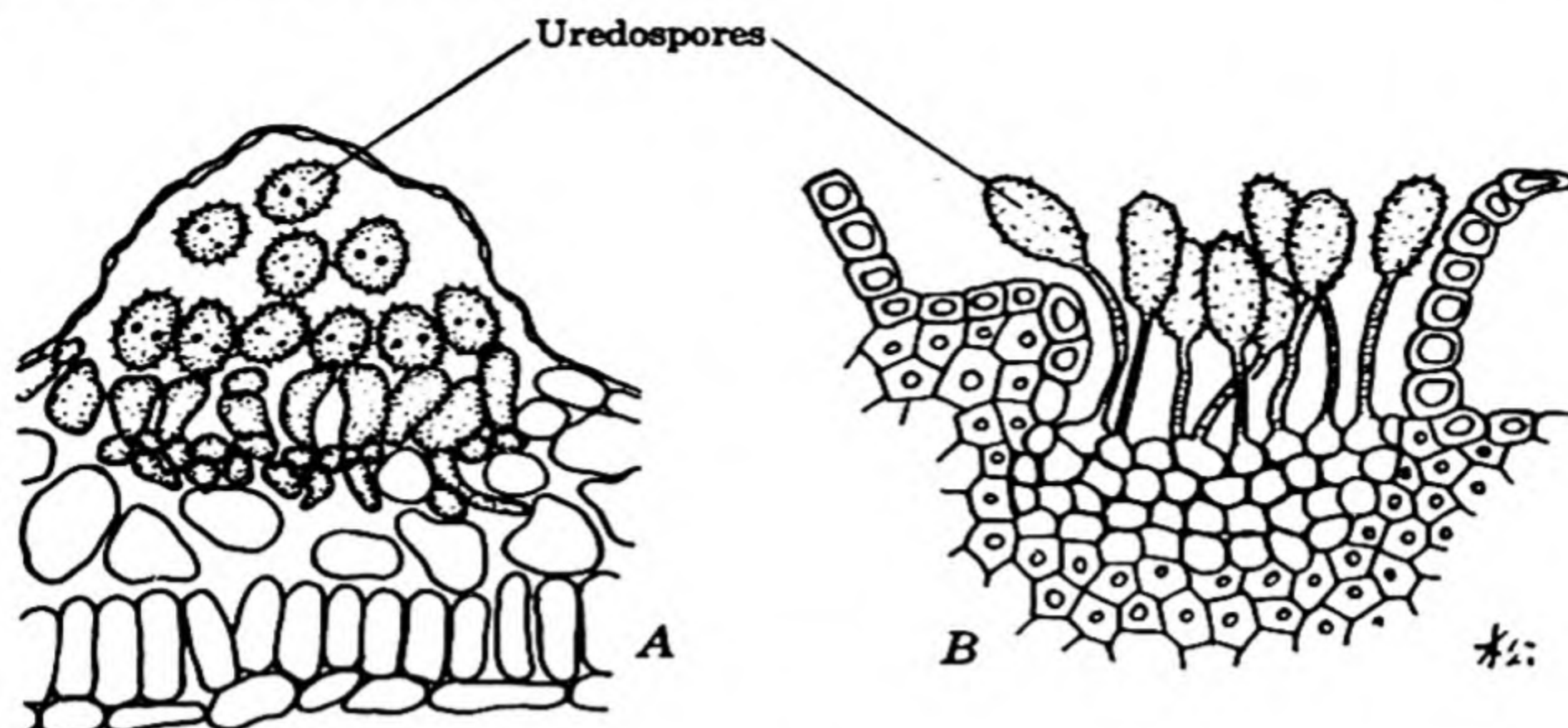


Figure 162. Two types of uredia. A. Uredospores produced successively one below the other; without stalks. B. Uredospores produced singly; stalked.

ferent rusts, and we base our classification of the Uredinales into families and genera largely on these teleutospore characteristics.

Teleutospores may be sessile or stalked; they may be completely free from one another or they may be embedded in a gelatinous matrix or united laterally, forming small groups, layers, or columns. If a teleutospore consists of more than one cell, each cell is capable of germinating into a promycelium as described on page 468. Teleutospores vary in color from almost colorless to a dark reddish brown; they vary in size and shape and in the external characteristics of their walls. Some teleutospores are smooth, some are spiny, and some are variously sculptured (Figure 163).

Sexual Compatibility in the Rusts. The sexual relations of the rusts have been investigated in relatively few species. The data available show that the rust species, as a group, are made up of self-sterile individuals and require two strains, $+$ and $-$, for sexual reproduction. Since the nuclei are haploid, some carry the $+$ factor and some the $-$ factor. In the binucleate mycelium one nucleus of each kind is present in each cell. These factors combine when karyogamy occurs in the teleutospore and segregate again at meiosis, so that two of the four basidiospores produced from each promycelium are $+$ and two are $-$. All the nuclei in the uninucleate mycelium therefore, being direct descendants of the basidiospore nucleus, are of the same strain. Consequently, the structures—spermatia and receptive hyphae—borne on the same mycelium carry the same factor.

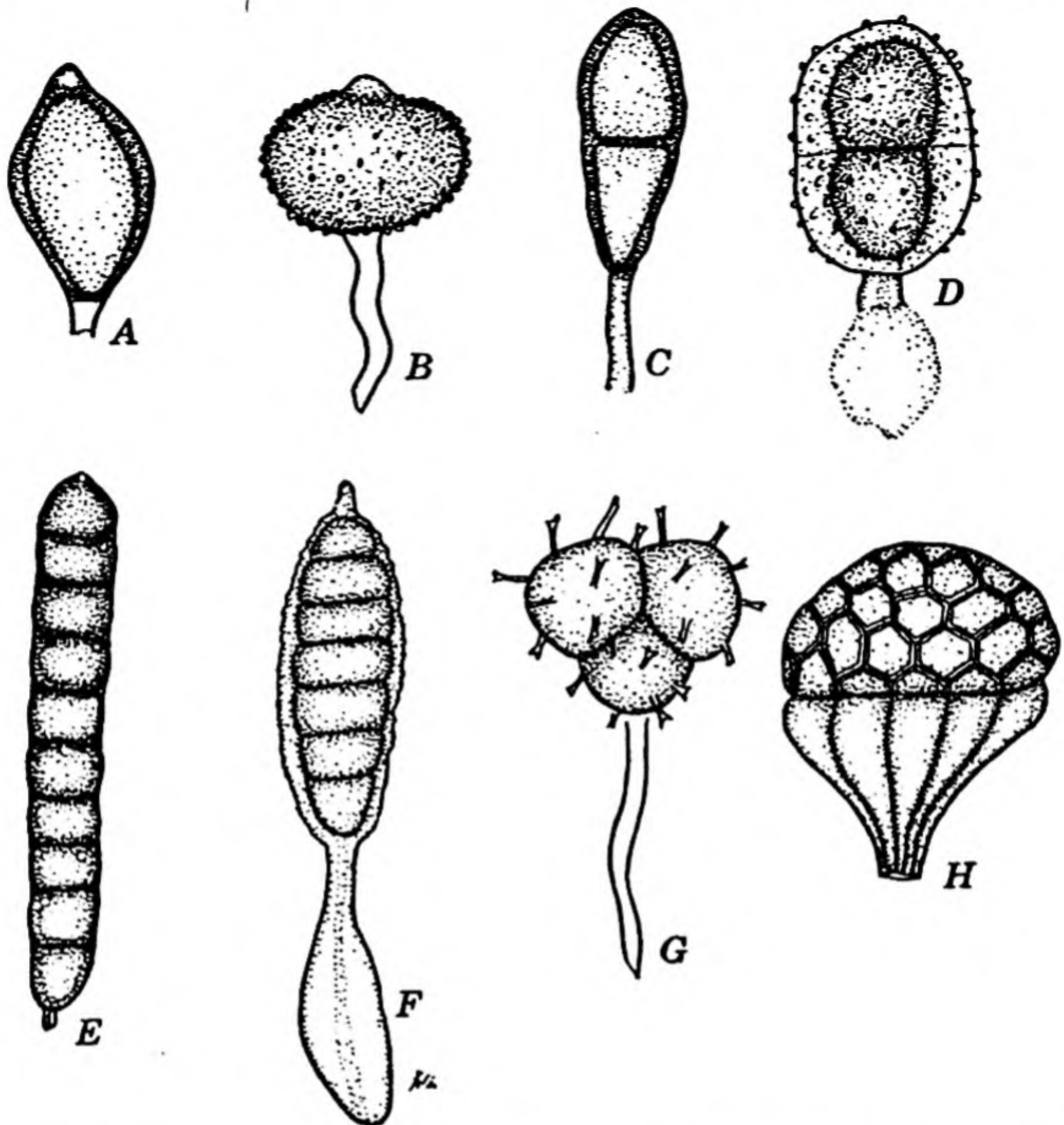


Figure 163. Various types of teleutospores representing eight genera of rusts as follows: A. *Uromyces*. B. *Pileolaria*. C. *Puccinia*. D. *Uropyxis*. E. *Xenodochus*. F. *Phragmidium*. G. *Nyssopsora*. H. *Ravenelia*. B, D, E, H, redrawn from Cummins by permission from *Manual of the rusts of the United States and Canada*, by J. C. Arthur, 1934, Purdue Research Foundation, Lafayette.

Plasmogamy, which initiates the binucleate condition, may take place by one or more of five methods described by Buller (1950). The most common of these methods are spermatization and the union of somatic hyphae within the host. Spermatization results from the union of a spermatium of one strain with a receptive hypha of the opposite strain. Somatogamy occurs when two uninucleate hyphae of opposite strains happen to meet in the tissues of the host.

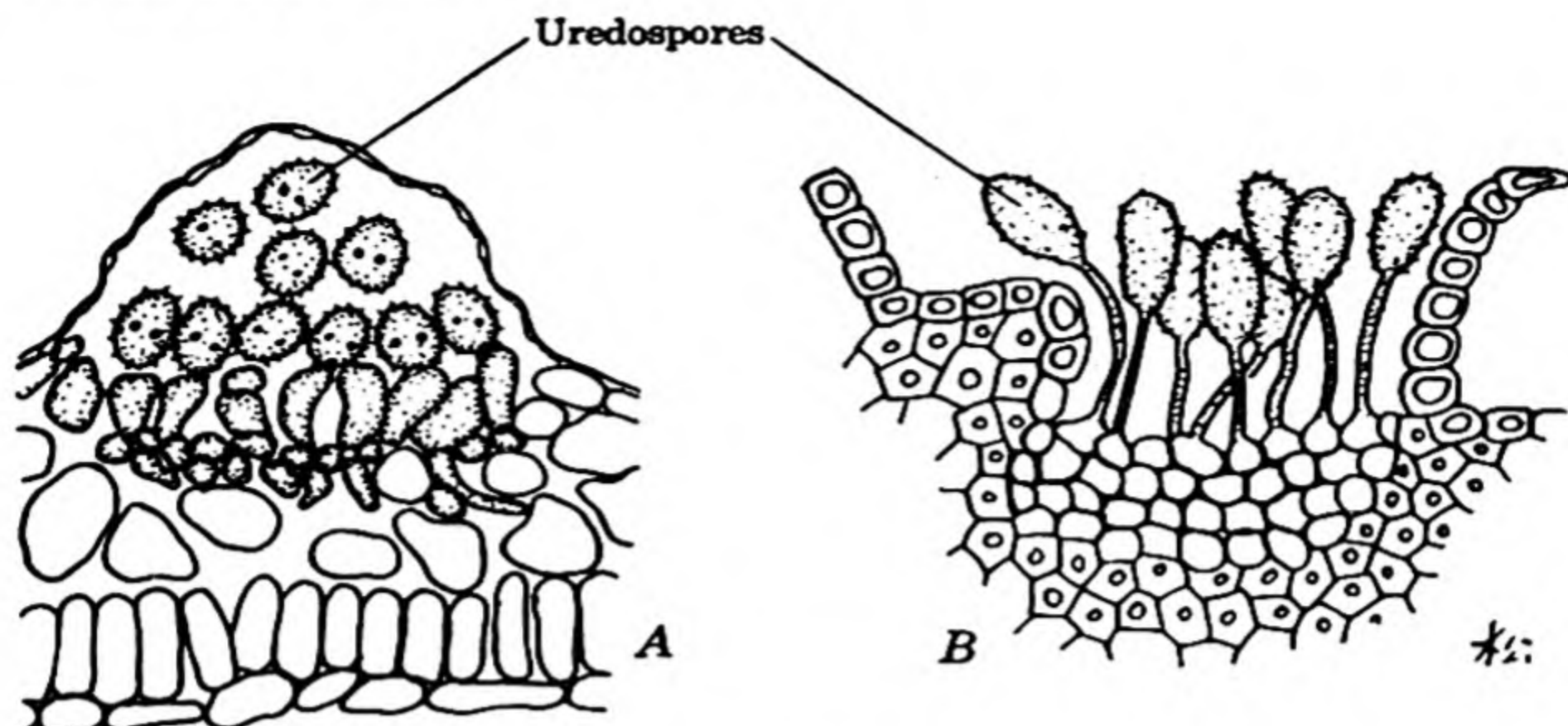


Figure 162. Two types of uredia. A. Uredospores produced successively one below the other; without stalks. B. Uredospores produced singly; stalked.

ferent rusts, and we base our classification of the Uredinales into families and genera largely on these teleutospore characteristics.

Teleutospores may be sessile or stalked; they may be completely free from one another or they may be embedded in a gelatinous matrix or united laterally, forming small groups, layers, or columns. If a teleutospore consists of more than one cell, each cell is capable of germinating into a promycelium as described on page 468. Teleutospores vary in color from almost colorless to a dark reddish brown; they vary in size and shape and in the external characteristics of their walls. Some teleutospores are smooth, some are spiny, and some are variously sculptured (Figure 163).

Sexual Compatibility in the Rusts. The sexual relations of the rusts have been investigated in relatively few species. The data available show that the rust species, as a group, are made up of self-sterile individuals and require two strains, + and —, for sexual reproduction. Since the nuclei are haploid, some carry the + factor and some the — factor. In the binucleate mycelium one nucleus of each kind is present in each cell. These factors combine when karyogamy occurs in the teleutospore and segregate again at meiosis, so that two of the four basidiospores produced from each promycelium are + and two are —. All the nuclei in the uninucleate mycelium therefore, being direct descendants of the basidiospore nucleus, are of the same strain. Consequently, the structures—spermatia and receptive hyphae—borne on the same mycelium carry the same factor.

KEY TO THE FAMILIES OF THE ORDER UREDINALES

- A. Teleutospore forming a septate promycelium upon germination
 - B. Teleutospores free or variously united, but never in the form of layers or crusts *Pucciniaceae*
 - BB. Teleutospores laterally united into layers, crusts, or columns *Melampsoraceae*
- AA. Teleutospores becoming septate during germination without the formation of an external promycelium *Coleosporiaceae*

The fact that the rusts have a polymorphic life cycle has complicated their classification a great deal. As in the Ascomycetes, but obviously to a greater degree, imperfect stages of most rusts are more likely to be encountered than perfect stages, at least at certain seasons. Since we base the classification of the rusts on the teleutospore, it is difficult to classify a rust if teleutospores are not available. The fact that in heteroecious rusts the teleutospores occur on a different host from that on which the aeciospores occur complicates matters further. The situation has been even more complex, because for a long time it was not possible to grow any rusts in artificial culture. Mycologists have had to resort, therefore, to the creation of an artificial "Uredinales Imperfecti" group in which the aecial and uredial stages are temporarily classified until the teleutospores are discovered. The form-genera *Caeoma*, *Aecidium*, *Peridermium*, and *Roestelia* designate different types of aecial stages on the basis of peridial features. *Caeoma* (Figures 161A, B) includes all aecial stages in which a peridium as such is lacking. The spores are formed as usual from a group of binucleate basal cells within the host tissues, and as the spore chains elongate they finally break through the epidermis of the host. A mass of aeciospores then appears on the surface, but the familiar cluster cups are lacking. *Aecidium* (Figures 161C, D) is the name we give to the aecial stages which produce their aeciospores in a structure shaped like a cup with a short, straight lip. In *Roestelia* (Figures 161E, F) the lip of the cup protrudes much beyond the surface of the host and soon becomes shredded, often bending back and forming an ornamental fringe around the mass of spore chains. The aecial lip of *Peridermium* (Figures 161G, H) is large and conspicuous. It is generally white or cream colored, and appears as a thin structure like tissue paper, protruding from the host.

The various form-genera of aecial stages described above show a degree of correlation with certain types of teleutospores. *Peri-*

dermium, for example, is associated with the teleutospores of the Coleosporiaceae and the Melampsoraceae; *Roestelia* is the aecial stage of a number of species in the genus *Gymnosporangium* of the Pucciniaceae; and *Caeoma* is mostly linked with such genera as *Gymnoconia* and *Phragmidium* of the Pucciniaceae. The most unpredictable relationships are those of *Aecidium*, which may be associated with a number of genera in the Pucciniaceae.

The form-genus *Uredo* includes all uredial stages.

The Uredinales Imperfecti are not included in the form-class Deuteromycetes because their characteristics are obviously uredinaceous and there is never a question as to the order to which their perfect stages will belong when found.

Excellent discussions of the phylogeny of the rusts are given by Bessey (1950), Savile (1954*b*, 1955), and Leppik (1953–1959).

family PUCCINIACEAE

The teleutospores of the Pucciniaceae are generally stalked. They may be borne free from each other, they may be embedded in a common gelatinous matrix, or they may be united into groups of three or more on a common stalk. The spore itself may be one-celled, two-celled, or many-celled. The walls are generally reddish brown, quite thick, and smooth or variously sculptured. A transparent, capsule-like sheath (Figure 163*D*) surrounds some teleutospores.

Teleutospore characteristics, aecial characteristics, and type of life history form the basis for the separation of genera in this family. Among economically important genera are the following. *Uromyces*, which has a one-celled teleutospore (Figure 163*A*), includes such parasites as *Uromyces appendiculatus* (bean rust), *Uromyces fabae* (broad bean rust), *Uromyces pisi* (pea rust), and *Uromyces caryophyllinus* (carnation rust). *Puccinia*, with a two-celled teleutospore (Figure 163*C*), includes *Puccinia graminis* (cereal rust), *Puccinia coronata* (crown rust of oats), *Puccinia asparagi* (asparagus rust), *Puccinia malvacearum* (hollyhock rust, also attacking many other malvaceous hosts), *Puccinia antirrhini* (snapdragon rust), and many others. *Gymnosporangium*, in which the two-celled teleutospores are embedded in finger-like or tongue-like gelatinous masses, includes, among other species, *Gymnosporangium juniperi-virginianae* (juniper, apple, and crab-apple rust), *Gymnosporangium globosum* (juniper, hawthorn, apple, and pear rust), and *Gymnosporangium sabinae* (juniper and pear rust). *Phragmidium*, with its many-celled teleutospore (Figure 163*F*), which has a long stalk

surrounded by a gelatinous sheath, includes a number of species on roses, raspberries, and other hosts. Many other rust genera which need not be mentioned here are described in such reference works as those of Arthur (1934), Grove (1913), McAlpine (1906), and Cummins (1959).

Puccinia graminis, a long-cycled, heteroecious rust, serves as a good example to tie together information on the Uredinales which we have discussed up to this point.

Puccinia graminis Pers.

The two-celled teleutospores (Figure 164P) which are produced in midsummer on the leaves and stems of susceptible grasses, such as wheat, barley, rye, oats, and red top, remain dormant until the following spring, passing the winter on the stubble in the fields. Overwintering takes place in the uninucleate, diploid stage after karyogamy has occurred. Early in the spring each cell of the teleutospore germinates and produces a promycelium (Figure 164R) into which the diploid nucleus migrates, undergoes meiosis, and forms four haploid nuclei. Septa are then laid down, separating the nuclei from one another into four cells. Each cell of the promycelium produces a sterigma on which a minute basidiospore is formed. The nuclei now squeeze through the sterigmata into the basidiospores. Two of the basidiospores are of one strain and two are of the other (Figure 164A).

Soon after their formation, the basidiospores are forcibly ejected by the water droplet method and are carried away by the wind. If they fall in a drop of water, the basidiospores germinate, producing slender germ tubes, but unless germination occurs on a common barberry bush (*Berberis vulgaris*) the germ tube soon dies for lack of food as the *barberry protoplasm is the only food which the mycelium resulting from a basidiospore is able to use in nature*.¹ Most basidiospores never reach a barberry bush and therefore perish, but those that happen to fall on barberries and germinate there (Figure 164B) carry on the life history of the fungus, their germ tubes penetrating into the tissues of the barberry and obtaining nourishment from the cell protoplasts through haustoria. Thus, a well-developed, branched, monokaryotic mycelium develops, its nuclei carrying the factor (+ or -) which the parent basidiospore happens to carry

¹ Of the several species of *Berberis* which are susceptible to the rust, *Berberis vulgaris* and *Berberis canadensis* are the only ones which grow wild in the United States.

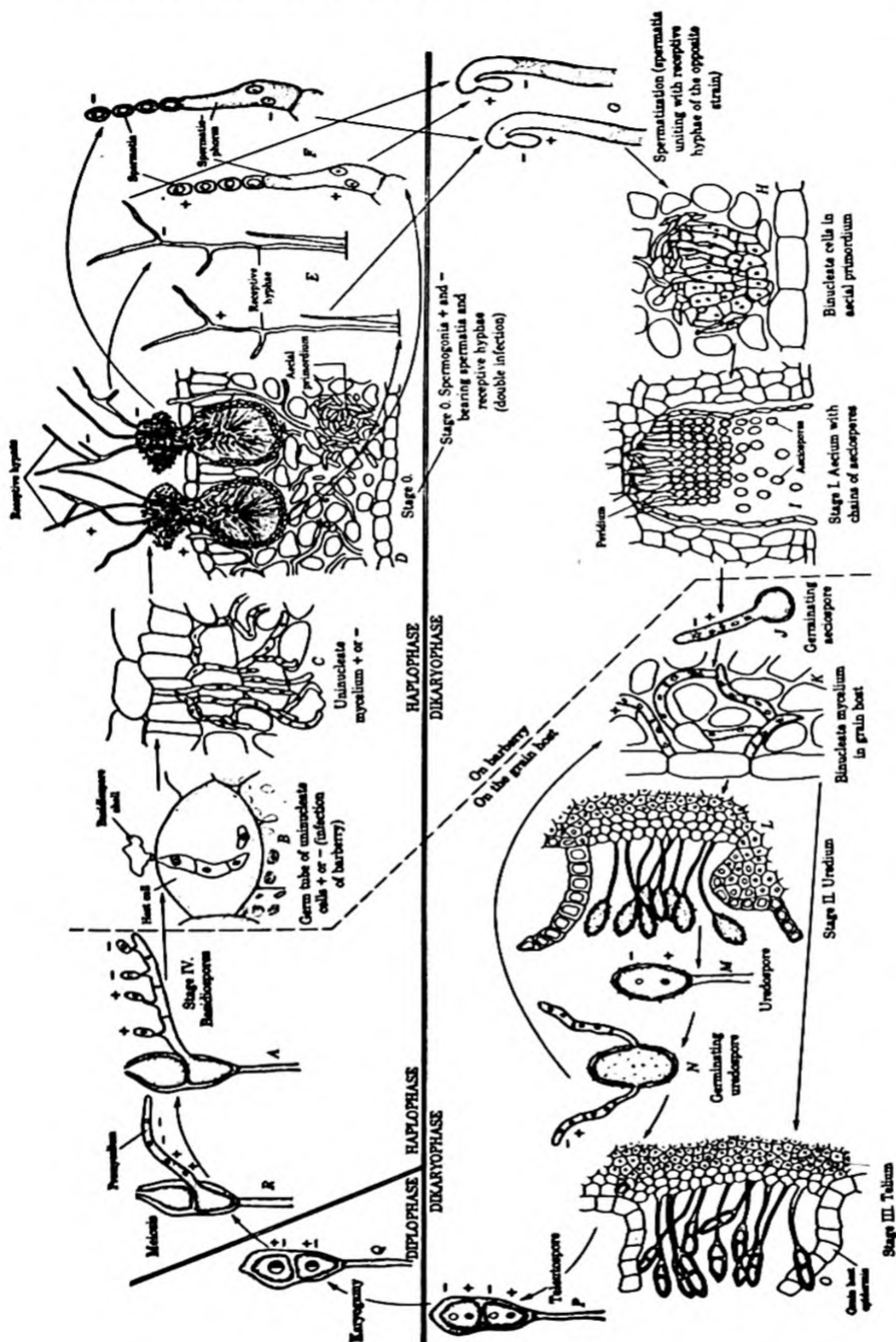


Figure 164. Life cycle of *Puccinia graminis*. A, J, K, N, R, constructed, diagrammatic; B, F, redrawn from Miss Allen, 1933, *Jr. Agr. Res.*, 47:1-16; C, H, redrawn from Lehman *et al.*, 1937, based on Miss Allen, 1930-1933; D, E, redrawn, by permission of the Toronto University Press and the Royal Society of Canada, from *Researches on fungi*, Vol. 7, by A. H. R. Buller, 1950, University of Toronto Press, Toronto; G, redrawn by permission of Macmillan and Co., London, from Buller, 1938, *Nature* (London), 141: 33-34.

(Figure 164C). In nature, it most often happens that several basidiospores at random will reach and infect the same barberry leaf so that both $+$ and $-$ mycelium will develop side by side and intermingle in the barberry tissues.

A few days after barberry infection, the hyphae of the fungus nearest the upper epidermis of the host develop spermogonia—in the manner already described—which open to the surface of the leaf (Figure 164D). Each spermogonium contains numerous spermatophores which cut off a succession of minute spermatia. These are exuded in small droplets of nectar from the opening above the spermogonium. Several periphyses are also formed in the upper part of the spermogonium. Each spermatium contains a large nucleus carrying the $+$ or $-$ factor, depending on the strain of mycelium which produced the spermogonium. All spermatia from a single spermogonium carry the same factor. The same mycelium which produces the spermatia also gives rise to receptive hyphae with the same genetic make-up as the spermatia. These arise in the spermogonia and protrude through the ostioles (Figures 164D, E). The spermogonial periphyses may also change to receptive hyphae. Since multiple infection is probably the rule in nature, spermatia and receptive hyphae, some of each carrying the $+$ factor and some the $-$ factor, are generally found on infected barberry leaves.

Spermatization now takes place through the agency of insects. A fly or some other insect, attracted by the fragrance of the spermogonial mass, visits it and sips the sweet nectar exuding from the ostioles. During this process spermatia in the nectar adhere to the mouth parts of the insect and are subsequently brushed off by the receptive hyphae and periphyses of the next spermogonium which the insect visits. If $+$ spermatia thus happen to be transferred to $-$ receptive hyphae or $-$ spermatia to $+$ receptive hyphae, spermatization is effected, the spermatial contents passing into the receptive organ by a pore dissolved in the walls at the point of contact (Figure 164G). Meanwhile the mycelium has penetrated the entire leaf, and the hyphae near the lower epidermis have formed a number of aecial primordia. The spermatial nuclei, which pass from the spermatia into the receptive hyphae, travel down the hyphae, pass through the septal perforations of the mycelium, and reach the cells of the aecial primordia, rendering them binucleate (Figure 164H). This is known to occur in *Puccinia helianthi* (Craigie, 1933, 1959), *Puccinia phragmitis* (Lamb, 1935), *Puccinia sorghi*, *Uromyces fabae* (Savile, 1939), *Scopella gentilis* (Payak, 1956), etc., and is almost certainly true of *Puccinia graminis* and

all other species of rusts which produce spermogonia. It has been demonstrated that aecial primordia (protoaecia) fail to develop into aecia unless and until spermatization takes place. On the other hand, it has also been shown that fusions of primary hyphae take place in *Puccinia graminis* within the leaf of the barberry.

Dikaryotization is followed by the formation of aecia and aeciospores. The latter are the first binucleate spores produced in the life history of the fungus. The aeciospore chains eventually break through the lower epidermis of the barberry, permitting the spores to escape (Figure 164I). Occasionally aecia may develop near the upper side of the leaf as well and break through the upper epidermis (Kadlubowska, 1953). The aeciospores are now disseminated by the wind and under favorable conditions germinate (Figure 164J). If germination occurs on a susceptible grass host, infection results and a binucleate mycelium develops (Figure 164K); but, if the aeciospore germinates elsewhere, the germ tube develops only until all the stored food in the spore is utilized, and then dies. Thus, aeciospores produced on the barberry can infect only the primary, i.e., grass, host.

Soon after infection, the binucleate mycelium in the grass host begins to form masses of cells, the uredia, from which binucleate uredospores arise on rather long stalks. The uredospores are oval, yellowish, and spiny. The pressure from the developing spores causes a break in the host epidermis, and an elongated streak-like rust-red pustule develops (Figure 164L). In masses, the uredospores appear rust-red, hence the name rust applied to these fungi and to the diseases which they cause. A field of highly susceptible grain which is heavily infected appears rusty, and a person walking through such a field comes away with his clothes covered with a rust-colored dust. The uredospores are the spores which perpetuate the fungus throughout the growing season. Since they are capable of germinating as soon as they mature, and of reinfecting the grass host on which they were produced, they spread from plant to plant and from field to field, and the disease soon reaches the magnitude of an epiphytotic. The uredospores, upon germination, produce binucleate mycelium which grows between the cells of the grass plant and in a few days produces new uredia and a new crop of uredospores. This repeating cycle of *Puccinia graminis* recurs several times in the spring and summer. About the time the grain is ripening, the uredia begin producing a few teleutospores. As the season progresses, more and more teleutospores and fewer uredospores are produced until finally only teleutospores are formed (Figure 164O)

The pustules which produce teleutospores are known as telia and constitute the black stage of the rust, the masses of dark red teleutospores appearing black to the unaided eye. The uredia thus gradually change into telia, but telia are also produced directly from the mycelium resulting from late uredospore infections.

Biological Specialization. The phenomenon of biological specialization which was discussed in connection with *Albugo candida* (page 70) has been extensively studied in the rusts, particularly in *Puccinia graminis*. A number of biological sub-species which differ only slightly in their morphology, but greatly in their ability to attack various grasses, constitute the species *Puccinia graminis*. To distinguish between these sub-species we have added a third name to the binomial *Puccinia graminis*, and designate each sub-species in the following manner:

Puccinia graminis tritici on wheat
Puccinia graminis hordei on barley
Puccinia graminis avenae on oats
Puccinia graminis secalis on rye

These and several other sub-species together make up the species *Puccinia graminis*. But, to complicate the situation further, each of these sub-species is made up of a large number of physiological races which differ in their parasitism on various agronomic varieties of the host. *Puccinia graminis tritici*, for example, consists of over 200 such races to which wheat varieties are differentially susceptible. All these physiological races and sub-species have the common barberry bush as their alternate host.

Interesting as this phenomenon of biological specialization is mycologically, its economic importance cannot be overemphasized. The only practical method of controlling cereal rust is by an extensive breeding program aimed to develop rust-resistant varieties of cereals. Obviously it is impossible to develop varieties that are resistant to all the physiological races of the parasite. Fortunately, however, there are relatively few races in a given geographical region which are violently destructive, and at these the plant breeder aims his program. Importation of new races into a region, of course, occurs occasionally and may seriously upset the breeding program if it is too narrow in scope. Another problem is presented to the plant breeder by the constant threat of the origin of new physiological races of *Puccinia graminis* by mutation and hybridization.

Barberry Eradication Campaign. The relationship of the barberry plant to wheat rust was suspected long before the study of fungi had

advanced to any degree. Early in the seventeenth century, French farmers noted that wheat planted in regions where barberry was abundant was seriously rusted. By 1660, a law was enacted in Rouen, France, ordering the eradication of barberry plants from the vicinity of grain fields. Two whole centuries passed before De Bary in 1865 showed the connection between the aecial stage on the barberry and the uredial and telial stages on the wheat. After the life history of the fungus was partially worked out, it became obvious that the eradication of the alternate host was the logical means of breaking the life cycle of the parasite and of reducing the incidence of rust in the grain fields. Indeed, the government of the United States launched such an eradication campaign in 1918, and statistics of the United States Department of Agriculture show that wheat rust epiphytotics have constantly decreased since the barberry eradication campaign was instituted. Dr. J. C. Walker of the University of Wisconsin gives an excellent summary of the history of barberry eradication in his book (1950) on plant pathology.

But the eradication of the alternate host not only breaks the life cycle of the fungus and thus lessens the incidence of infection, it also reduces the possibility of new physiological races by hybridization, since plasmogamy (by spermatization or somatogamy) occurs mostly on the barberry where the uninucleate mycelium grows. The function of the spermatia and their role in dikaryotization were discovered only in 1927 and were announced in an epoch-making paper by Dr. J. H. Craigie of the Dominion Laboratories in Ottawa, Canada. Since then, several mycologists in this country and abroad have shown that physiological races and biological forms of the organism can and do hybridize, producing new races.

Even complete eradication of the barberry, however, will not result in the disappearance of wheat rust, for in the warmer regions the fungus can survive over the winter in the uredospore stage and infect the grain directly without need of an alternate host. Overwintered uredospores may be blown in large numbers to northern wheat fields and infect the plants. Even so, by the time they reach northern regions in any quantity, the season is advanced.

Unfortunately for the plant breeder it has been discovered that nuclear exchanges can and do occur also between dikaryotic mycelia on the grain host during the uredial stage. Both genetic (Nelson, 1956; Watson, 1958) and morphological (Rodenhisser and Hurd-Karrer, 1947; Wilcoxson *et al.*, 1958) evidence has shown that dikaryotic hyphae originating from uredospores of different races of *Puccinia graminis* may fuse and exchange nuclei.

genus GYMNOSPORANGIUM

The familiar reddish balls we call cedar apples, which decorate many junipers as ornaments do a Christmas tree, are galls caused by the mycelium of any one of a number of species of *Gymnosporangium*. These galls (Figure 165), composed of host tissue penetrated by mycelium, bear the telia of the fungus. The fungus overwinters in the cedar apples as binucleate mycelium. In the spring, the telia absorb water and expand into long finger-like or thick, tongue-like, reddish, gelatinous structures in which teleutospores by the hundreds are embedded.



Figure 165. "Cedar apple" with telia of *Gymnosporangium juniperi-virginianae*. Photograph courtesy F. C. Strong, 1948, *Mich. Agr. Exp. Sta. Quart. Bull.*, 30:283-288.

Gymnosporangium juniperi-virginianae and *Gymnosporangium globosum*, both of which are quite common, are among the species which produce their telia on the juniper (*Juniperus*). Both form their spermogonia and aecia on the apple and crab apple, and *Gymnosporangium globosum* in addition forms them also on the hawthorn (*Crataegus*). No uredial stage occurs in these two species, nor indeed in most other species of *Gymnosporangium*. The aecia of both species of *Gymnosporangium* mentioned above are of the *Roestelia* type (Figures 161E, F). With no repeating stage existing, it is relatively easy to break the cycle of these fungi by the eradication of one host from the vicinity of the other. In other words, do not plant junipers close to your apple orchard if you prefer apples to cedar apples.

family MELAMPSORACEAE

The Melampsoraceae produce their teleutospores united laterally in the form of crusts or columns. The spores germinate into septate promycelia as described for the Pucciniaceae.

Cronartium ribicola, the cause of white-pine blister rust, is the best-known example of this family. It is a long-cycled heteroecious rust in which the teleutospores are united in long columns which protrude from the underside of the leaves of currants and gooseberries, the primary hosts. Stages 0 and I of *Cronartium ribicola* are produced on the white pine. The spermogonia (Figure 160A) are formed in the cortical region of the infected branches. They cover a large area as compared with the minute spermogonia of *Puccinia graminis* we have studied. Although small blisters are caused by the spermogonia, the prominent blisters which give the disease its name are caused by the aecia as they break through the tissues to the surface. The prominent, white or cream-colored, flaring, peridial lip of the aecium (*Peridermium*) is clearly visible (Figures 161G, H).

The primary uninucleate mycelium, which produces the spermogonia and aecia, is perennial in the tissues of the white pine, and the fungus passes the winter in the mycelial stage. The aeciospores infect currants and gooseberries, and produce binucleate mycelium which gives rise to uredia and telia. These protrude from the underside of the leaf, breaking through the lower epidermis. Under a magnifying glass, the uredia look like minute, brown, dome-shaped igloos. The telia are elongated, often curved, horn-like columns consisting of long teleutospore cells united laterally and terminally (Figures 166, 167). These germinate in place, the same season they are formed, and produce promycelia each with four basidiospores.

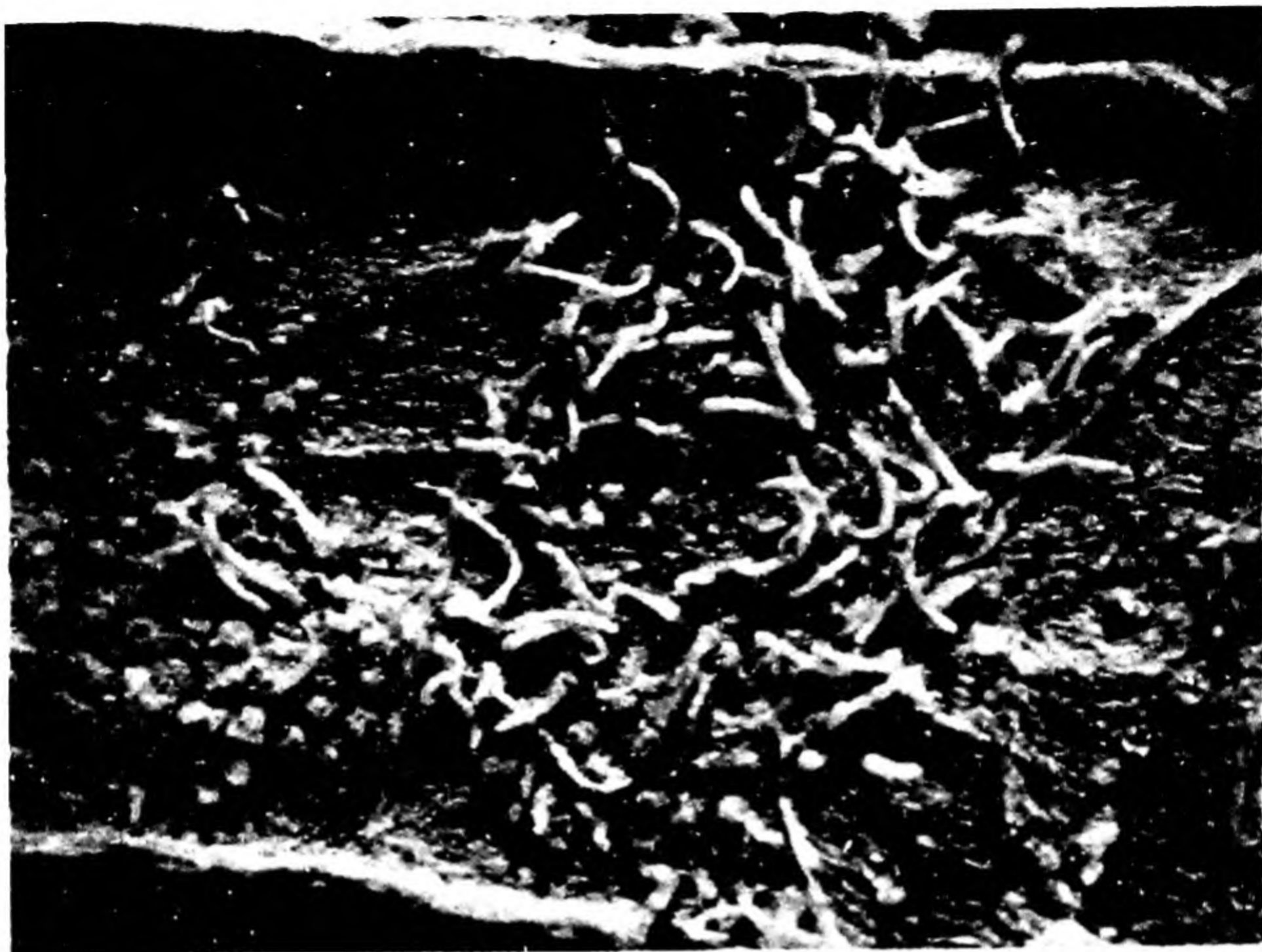


Figure 166. Photograph of telia of *Cronartium ribicola*, greatly magnified (See Figure 167 for cellular structure.) Photograph by Fred W. Kent.

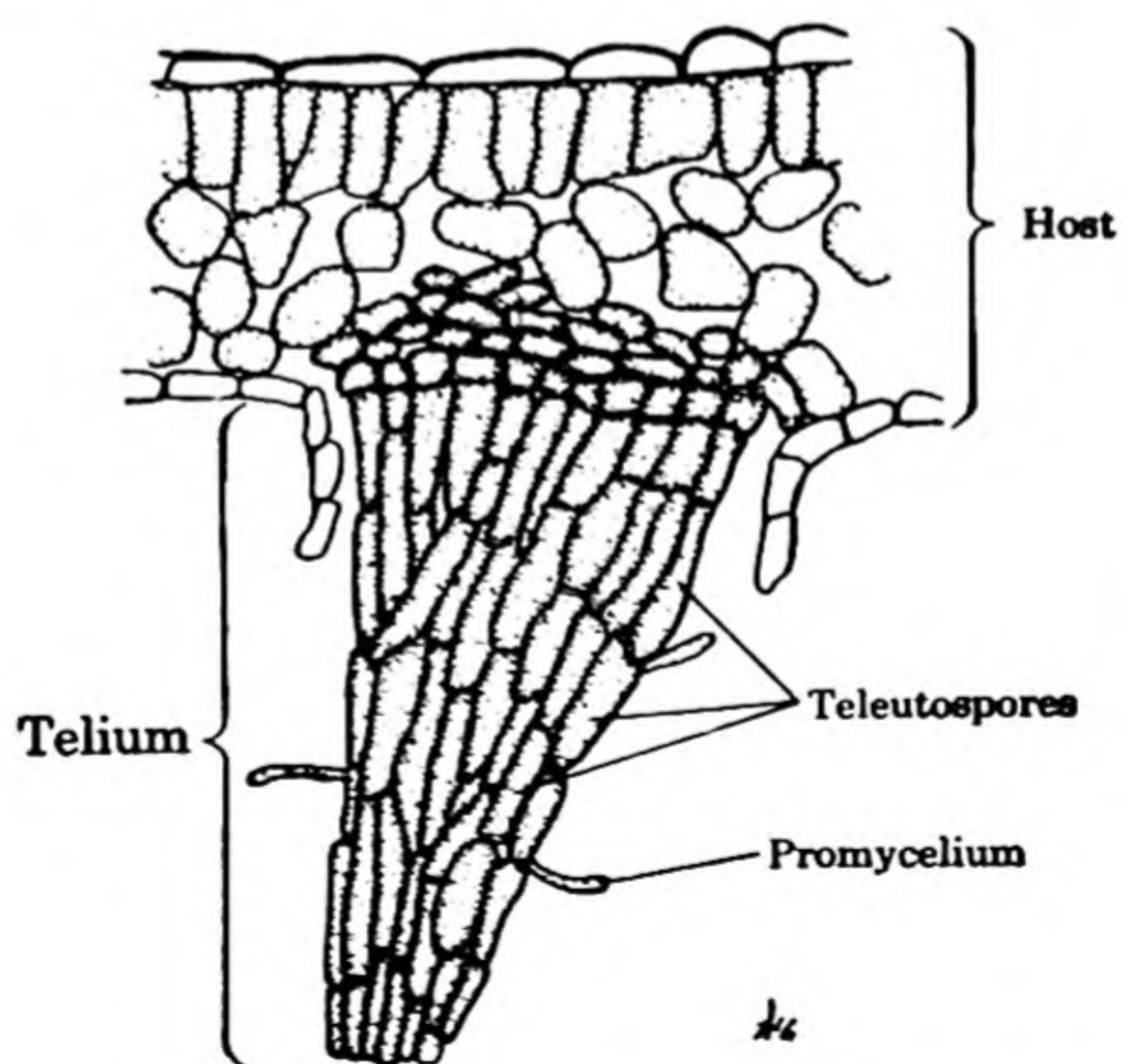


Figure 167. Telium of *Cronartium ribicola*.

The basidiospores are scattered by the wind; those that reach white pine trees cause infection if conditions are favorable.

Since the white pine is the economically important host, it is the currants and gooseberries that we attempt to eradicate in order to break the life cycle of the parasite. The campaign which plant pathologists of the United States Division of Forestry are conducting has been quite successful. An advantage which man has over this fungus is that the repeating (uredial) stage is not on the economically important host, as it is in *Puccinia graminis*.

family COLEOSPORIACEAE

The teleutospores of members of this family are united laterally, forming crust-like layers on the host. No external promycelium is produced from the teleutospores. Instead, karyogamy and meiosis occur within the teleutospore which then becomes four-celled by the formation of three cross-walls.

Coleosporium solidaginis, a rust which you can collect easily on the leaves of goldenrod (*Solidago*) in the summer, produces its uredia and telia on that host and its spermogonia and aecia on various pines. The aecia form abundantly on the pine needles, and you can easily recognize them by the prominent white lip which places them in the form-genus *Peridermium*.

THE SMUTS

order USTILAGINALES

The smuts are so called because they form black, dusty spore masses which resemble soot or smut.

General Characteristics. The smuts are normally parasitic on plants, but they are not obligate parasites. We have grown many smuts in culture, and we have induced a few to complete their entire life cycle—from teleutospore to teleutospore—on artificial media.

The smuts resemble the rusts in several ways, and the two orders appear to be closely related. The main features of the two orders may be compared and contrasted as follows:

1. Both groups produce teleutospores, but
 - a. the teleutospores of the rusts are formed from terminal cells of the mycelium, whereas
 - b. the teleutospores of the smuts are usually formed from intercalary cells.

2. Basidiospores are produced from the germinating teleutospores of both groups, but
 - a. the basidiospores of the rusts are borne on sterigmata in definite numbers, usually four, and are discharged violently, whereas
 - b. the basidiospores of the smuts are not borne on sterigmata, are not produced in definite numbers, and are not violently discharged.
3. Most species in both orders lack basidiocarps, but
 - a. one small family, the Graphiolaceae, which we generally classify in the Ustilaginales, does produce cup-like structures in which the teleutospores develop.
4. The mycelium of both groups, in general, is intercellular and obtains nourishment by means of haustoria.
5. The dikaryotic mycelium of both groups is known to produce clamp connections, but
 - a. clamp connections are rare in the rusts, whereas
 - b. clamp connections are more common in the smuts.

Occurrence, and Importance to Man. The Ustilaginales or smuts constitute an order of fungi which has representatives all over the earth. Certain species are geographically confined to relatively small areas, but others are found wherever their hosts grow. The universally distributed *Ustilago maydis* (corn smut) and the equally widely occurring *Ustilago avenae* (loose smut of oats), *Tilletia caries* and *Tilletia foetida* (bunt or stinking smut of wheat), as well as *Urocystis cepulae* (onion smut), are common examples of the smut fungi which you can find almost anywhere.

Economically, the smuts are very important, causing millions of dollars' worth of damage to crops. Many of the widely distributed smuts cause serious diseases of cereal crops; bunt, for example, presents as great a world problem as wheat rust.

Smut spores, which may accumulate in a threshing machine, occasionally create a smut dust which may explode violently, destroying machines and grain by fire.

Somatic Structures. The mycelium of the smuts, parasitic in nature on flowering plants, does not develop so profusely as that of many other parasitic fungi, although it does spread to a considerable degree within the host. The hyphae as a rule are intercellular, but in some species such as *Ustilago maydis*, they are intracellular as well. Haustoria which penetrate the host cells from the intercellular hyphae are present in some species, but are lacking in others.

The primary mycelium which originates from the germinating basidiospores or conidia appears to be of relatively short duration, dikaryotization generally taking place soon after its formation. In the ab-

sence of plasmogamy, the primary mycelium seldom develops very extensively. The secondary mycelium, the cells of which are binucleate, constitutes the important somatic phase of these fungi. Clamp connections are present in the mycelium of several species.

At the time of sporulation, the mycelium develops profusely in certain portions of the host, lays down many septa, and forms masses of hyphae. These hyphal masses are converted into large, dusty sori, which may or may not be covered by a membrane. These are the smut balls which contain the teleutospores, as will be described below.

Mycelium generally does not develop in artificial culture, the smut colonies consisting of masses of yeast-like cells which reproduce by budding and form giant yeast colonies. However, mycelium has been obtained in culture in a number of species.

Asexual Reproduction. Asexual reproduction is by means of conidia produced both from uninucleate and from binucleate mycelium. Conidia are often borne on sterigmata and may be forcibly ejected in the same manner as the basidiospores of other Basidiomycetes. Such phenomena make it difficult to homologize these structures in the smuts with the undoubted conidia and basidiospores of other fungi, and as a result there is considerable controversy and confusion in the terminology employed by various authors.

Budding is a very common method of asexual reproduction in the Ustilaginales. Both basidiospores and conidia bud repeatedly in a yeast-like fashion, in nature as well as on artificial media.

Sexual Reproduction. The Ustilaginales possess no sex organs. Plasmogamy takes place by the fusion of almost any two compatible cells. Two basidiospores may copulate, or two conidia, or daughter buds of these structures. Mycelial hyphae may also fuse, giving rise to the dikaryotic condition, and basidiospores or buds from them may fuse with hyphae. Any or all of these methods may be employed under different conditions by almost any species of smut, the environment often determining the behavior of the cells with regard to sexual fusions.

Compatibility in the smuts appears to be extremely complex, and many explanations have been offered for the results of genetic experiments. Rowell (1955), working with *Ustilago maydis*, concluded that compatibility is governed by two pairs of factors a and b, the former with two alleles a^1 and a^2 , the other with multiple alleles $b^1 \dots b^n$. It is the a factors, according to Rowell, that govern cell fusions. Vaheduddin (1942) reported some sixty-six "sex groups" (mating types) in *Sphacelotheca sorghi*. From the very large number of extant stud-

ies some authors conclude that both bipolarity and tetrapolarity have been well established in the Ustilaginales. Whitehouse (1954), however, believes that the compatibility mechanism in the smuts is bipolar, and that erroneous reasoning is responsible for all claims of tetrapolarity. A large number of investigators experimenting with smuts have built a considerable literature on the genetics of these organisms (Fischer, 1951a; Fischer and Holton, 1957). Foremost in this country are Professors E. C. Stakman, J. J. Christensen, and their coworkers at the University of Minnesota, and Professors C. S. Holton and G. W. Fischer at Washington State University at Pullman.

Teleutospores and Basidiospores. The teleutospores or so-called smut spores are the characteristic structures of the Ustilaginales. When the binucleate mycelium reaches the sporulation stage, it usually forms masses of hyphae composed of numerous short cells. The protoplast of each hyphal cell rounds up and the hyphal walls gelatinize. Each protoplast secretes around itself a thick wall which eventually converts the protoplast into a round teleutospore completely free from its neighbors but closely packed together with them in a sorus. The teleutospores of these smuts, therefore, are formed somewhat in the manner of chlamydospores, and for this reason some authors refer to smut spores in general as chlamydospores instead of teleutospores.

The individual teleutospores are typically globose, and yellow to brown; their walls are spiny, reticulate, or smooth. In many species the spores are entirely free from each other, but in some species they have a tendency to cling together in pairs or larger groups which are separated easily by the application of a little pressure, or which may be more difficult to separate. In other species, several teleutospores are cemented together and form specialized spore balls. These are often differentiated into fertile and sterile regions, the cells of the fertile regions alone being capable of germination. These various arrangements of teleutospores are used as a basis for the separation of genera (Figure 168).

Many studies on teleutospore germination have shown that, contrary to the situation found in other fungi, spore germination in most Ustilaginales is favored by low temperatures. One study, that of Meiners and Waldher (1959), shows that nine species of *Tilletia* had an optimum temperature for spore germination of 5° C., whereas three other species had optima of 5–10°, 10°, and 15°, respectively. These workers also confirmed previous studies on the effect of light on

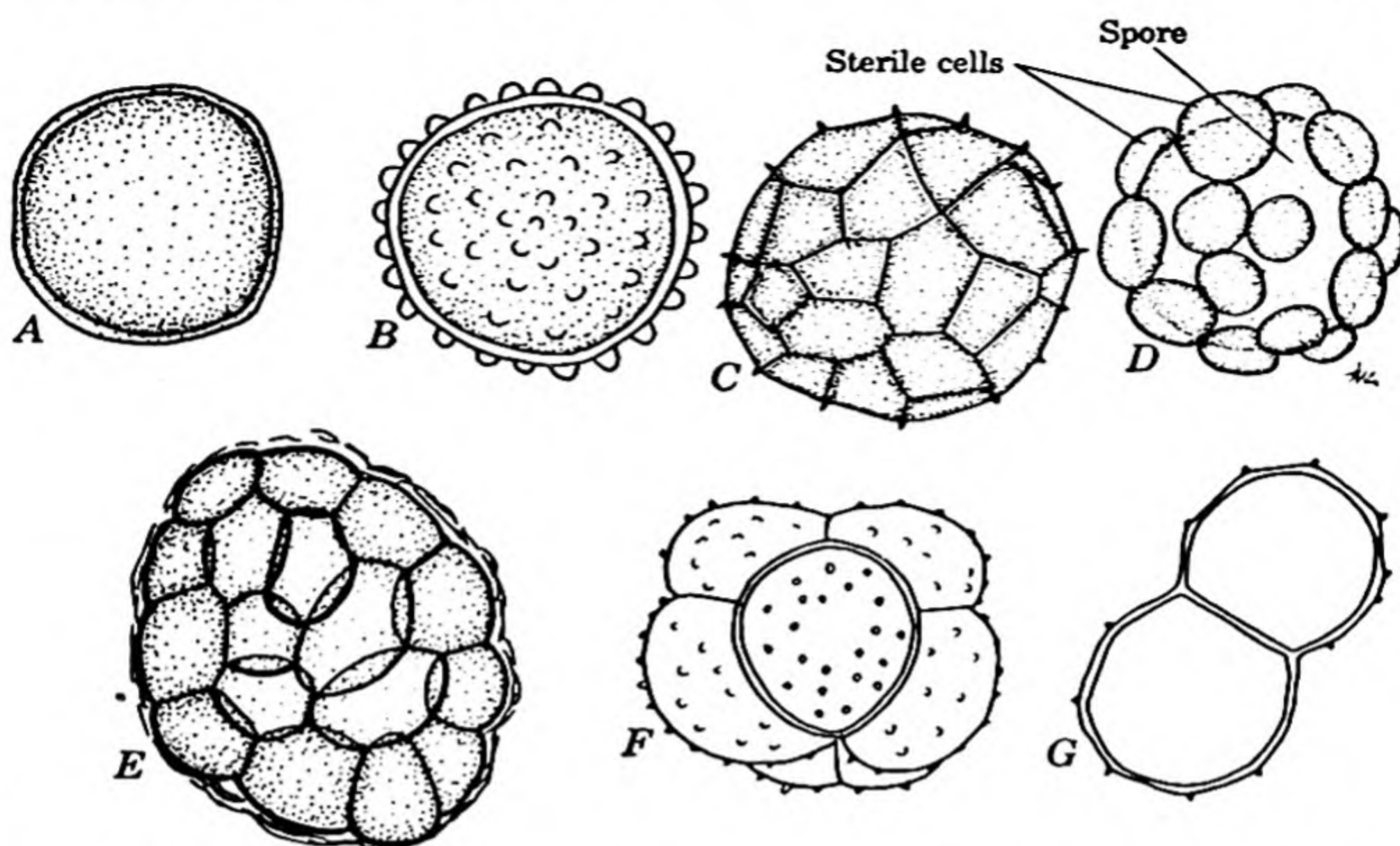


Figure 168. Various types of smut spores (teleutospores). A. *Ustilago levis*. B. *Ustilago maydis*. C. *Tilletia caries*. D. *Urocystis cepulae*. E. *Tuburcinia trientalis*. F. *Thecaphora seminis-convolvuli*. G. *Schroeteria delastrina*. E–G, redrawn by permission from *The British smut fungi*, by G. C. Ainsworth and Kathleen Sampson, 1950, Commonwealth Mycological Institute, Kew, Surrey.

teleutospore germination. Light stimulated germination in five species, suppressed germination in two, and had no effect in three.

The teleutospores of the smuts are homologous to those of the rusts, which we have already discussed. The spore itself is to be regarded as an encysted probasidium in which karyogamy and meiosis occur. At the time the spore germinates we may think of the probasidium as having evolved into the hypobasidium, which now gives rise to a short epibasidium (promycelium) usually of determinate growth, on which basidiospores (often called sporidia) are produced. The method of germination and the type and behavior of the basidiospores are characters on the basis of which we subdivide the order Ustilaginales into families.

Classification. The order Ustilaginales is subdivided into three families, two of which are large, well known, and widely distributed, and the last of which is small, relatively unknown, and more or less confined geographically. These are the Ustilaginaceae, the Tilleti-

aceae, and the Graphiolaceae. They are distinguished on the basis of the following characteristics:

- A. Basidiocarps absent
 - B. Promycelium septate; basidiospores produced laterally from each cell of the promycelium *Ustilaginaceae*
 - BB. Promycelium non-septate; basidiospores in a terminal cluster *Tilletiaceae*
- AA. Cup-shaped basidiocarp produced *Graphiolaceae*

Fischer's *Manual of North American Smut Fungi* (1953) is now the authoritative taxonomic treatise for this part of the world. Zundel's *The Ustilaginales of the World* includes descriptions of all species known up to 1953. Another monumental taxonomic treatise on smuts is Savulescu's two-volume work on the smuts of Romania.

family USTILAGINACEAE

In the Ustilaginaceae, the young binucleate teleutospore undergoes karyogamy and becomes a uninucleate, diploid spore at maturity (Figure 169B). This spore may germinate immediately, or it may require a dormant rest period before germination can take place. At the time of germination, the spore wall cracks open and the promycelium issues forth in the form of a short germ tube. The zygote nucleus soon migrates into the promycelium, undergoes meiosis, and the four resulting haploid nuclei distribute themselves more or less uniformly in the promycelium. In some species reduction-division occurs in the teleutospore and the nuclei migrate in the promycelium which issues from the spore (Figures 169C, D). Septa are now laid down separating each nucleus from its neighbors, so that the septate promycelium now consists of uninucleate cells. As each nucleus divides by mitosis, one daughter nucleus migrates into a bud which develops at the side of each promycelial cell, and the other remains in the cell. These uninucleate buds are the basidiospores (often called sporidia) (Figures 169F, G). In bipolar or tetrapolar species, the genetic factors controlling sexual compatibility segregate at the time of meiosis so that the basidiospores are of different strains.

The next step in the life history, after discharge of the basidiospores, varies with the species. In some species budding of basidiospores takes place and then two secondary basidiospores of opposite strain may copulate; in other species a basidiospore of one strain may unite with a hypha issuing from a basidiospore of the opposite strain; in still other species, as in *Ustilago maydis* (corn smut), the basidio-

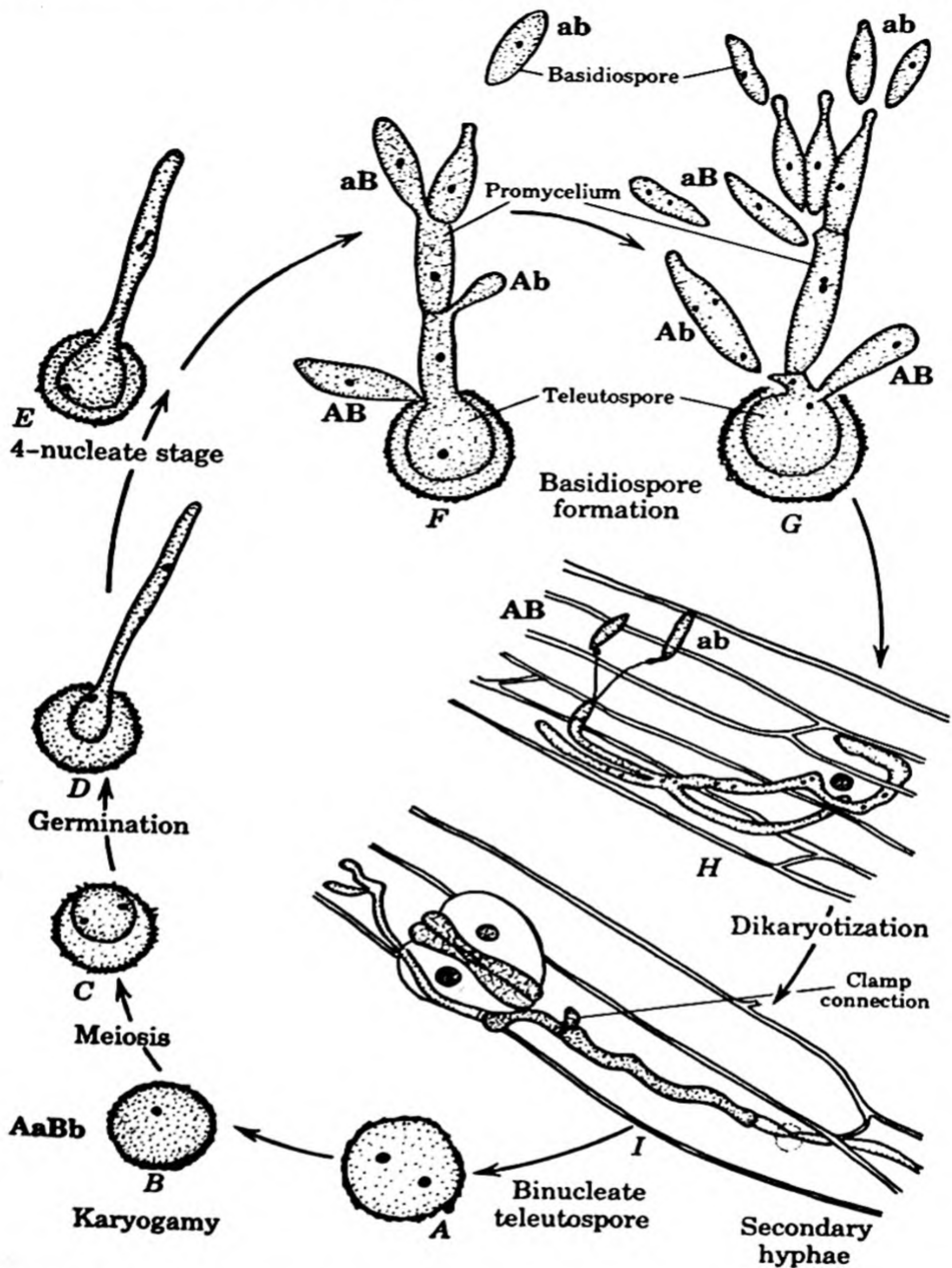


Figure 169. Life cycle of *Ustilago maydis*, showing possible segregation of the compatibility genes $AaBb$. A, constructed; C-I, redrawn from Hanna, 1929, *Phytopath.*, 19:415-442.

spores first germinate and produce a uninucleate mycelium which infects the host, and then dikaryotization takes place within the host by means of hyphal fusions (somatogamy) (Figure 169H). In some species conidia are produced from the uninucleate hyphae and unite with hyphae of the opposite strain. In a few forms, such as *Ustilago tritici* (loose smut of wheat), no basidiospores are produced, but the cells of the promycelium germinate into hyphae.

Regardless of how dikaryotization takes place, it is the binucleate mycelium which carries on the life history of the fungus. The uninucleate mycelium seems to be of short duration and seldom grows very much. Normally, it bears no clamp connections and forms no teleutospores. The secondary mycelium in the host may produce branches which reach the surface of the host and there give rise to several crops of binucleate conidia which are disseminated by the wind and initiate new infections. Later, the binucleate mycelium forms smut balls (sori) in which teleutospores develop as previously described. Generally, no symptoms appear on the infected host until the smut balls are formed. The smut fungi overwinter either in the teleutospore stage or as mycelium in the host. In a perennial host, the smut mycelium may invade the crown of the host, pass the winter there, and in the spring grow into the new shoots, which are thus infected from their very beginning. The fungi which cause loose smut of various grains (*Ustilago tritici*, *Ustilago avenae*, etc.) invade the ovaries of the host at blossom time, and develop very slowly while the seed is maturing. The mycelium remains dormant in the seed. When the seed germinates, the mycelium grows in the tissues of the seedling and eventually sporulates in the flower head, destroying the flowers and replacing the grain with masses of smut spores.

family TILLETIACEAE

The Tilletiaceae differ from the Ustilaginaceae in the method of teleutospore germination. The diploid nucleus of the mature teleutospore undergoes meiosis at the time of germination (Figure 170B). A mitotic division typically follows and results in the formation of eight haploid nuclei which migrate into the promycelium issuing forth from the teleutospore (Figure 170C). This promycelium, in contrast to that of the Ustilaginaceae, does not become septate. Instead, a number of basidiospores, typically eight, are formed at the tip of the promycelium and one nucleus migrates into each. These basidiospores are of at least two strains, half of them carrying the A, the other half the a, factor for sexual compatibility. Copulation tubes

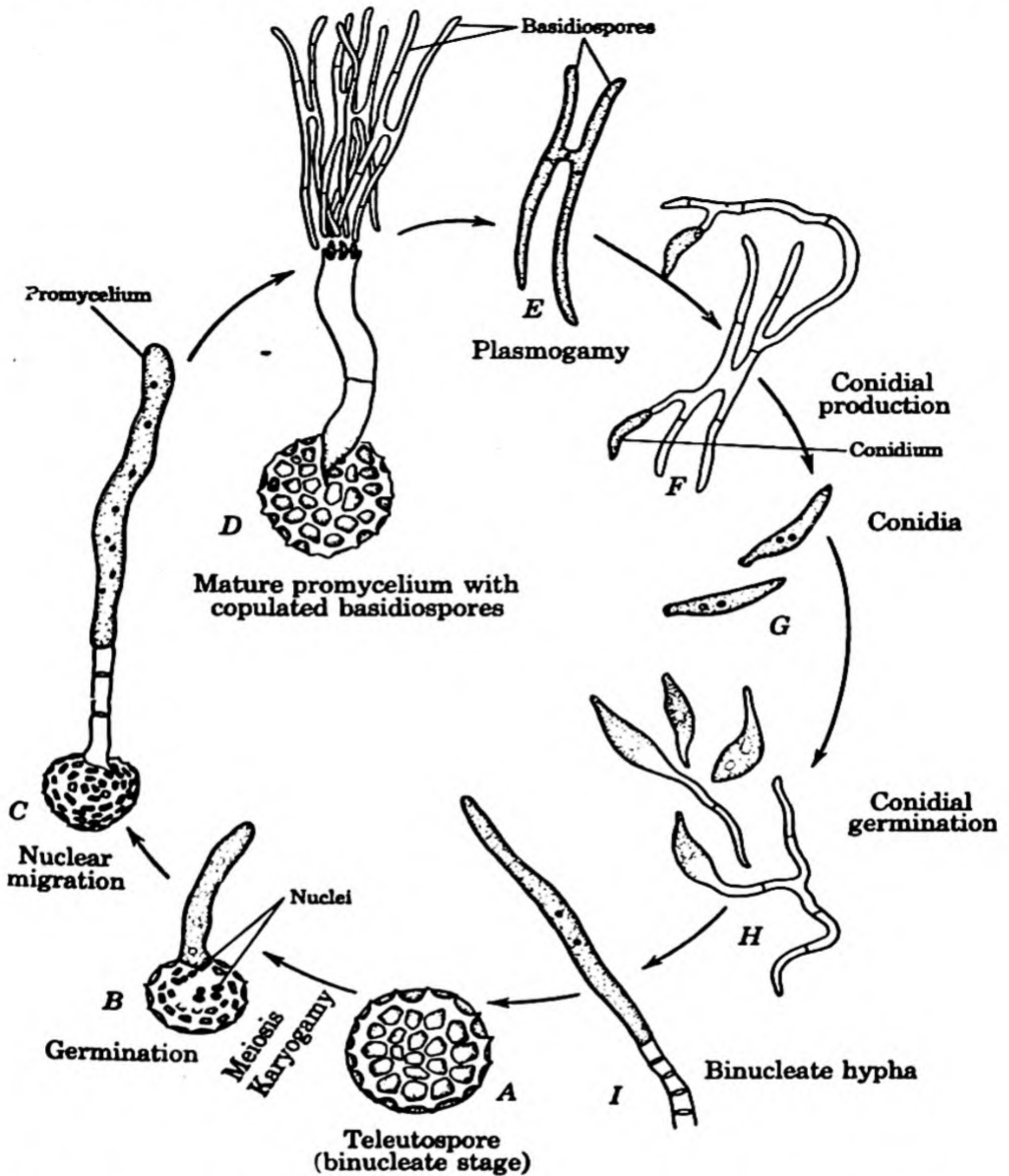


Figure 170. Life cycle of *Tilletia caries*. B, C, E, G, I, redrawn by permission of the authors from *Bunt or stinking smut of wheat* (planographed), 1941, Holton and Heald, Burgess Publishing Co., Minneapolis; D, F, H, redrawn by permission from *Manual of plant diseases* by F. D. Heald, 1926, McGraw-Hill Book Co., New York.

now develop between two compatible basidiospores, uniting them into H-pieces while they are still attached to the promycelium (Figure 170D). Plasmogamy then takes place between the two members of the H-piece, one protoplast migrating through the tube into the other basidiospore (Figure 170E). Crescent-shaped conidia generally develop on sterigmata produced by the binucleate member of the H-piece; the nuclei divide conjugately, and one pair passes into the conidium (Figure 170G). Upon discharge and germination, the conidia develop binucleate mycelia which infect the host. Eventually, this mycelium produces the smut balls of teleutospores (Figure 170A). Binucleate mycelium issuing from the binucleate member of the H-piece may also infect the host directly. This general life history pattern varies frequently. For a complete discussion of the life history of these fungi and the whole problem of the smuts, read Fischer and Holton's excellent *Biology and Control of the Smut Fungi* (1957).

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21 sub-class HOMOBASIDIOMYCETIDAE mushrooms, shelf fungi, coral fungi, puffballs, earthstars, stink- horns, bird's-nest fungi

Introduction. The fungi included in the sub-class Homobasidiomycetidae, are the ones which most people know best. Because of their size, the fruiting bodies of these fungi are familiar to anyone who takes an interest in living things. Anyone who tramps in the woods in the spring or fall sees mushrooms, shelf fungi, and small puffballs growing on old stumps or logs, or on the ground; farmers encounter large puffballs in their pastures, city dwellers find them on their lawns, and golfers see them on the greens. The mushrooms in the neat, cellophane package at the local supermarket are now a commonplace article. Earthstars, stinkhorns, and bird's-nest fungi are somewhat less common, the last probably unknown to most people because of their smaller size. All these examples are, of course, the basidiocarps of the fungi, whose main body, in the form of mycelium, goes unnoticed in most instances. The complexity of the basidiocarps and the formation of specialized reproductive and even somatic tissues support the theory that the Homobasidiomycetidae are probably the most advanced of all the fungi on the scale of organic evolution.

The chief characteristic of the Homobasidiomycetidae is their typically club-shaped, non-septate basidium (holobasidium), which usually bears four basidiospores on sterigmata, but may bear only one or as many as eight. All Homobasidiomycetidae produce such basidia one time or another. It is the manner in which such basidia are borne, *i.e.*, the organization of the basidial layer, which distinguishes among the various orders and families within this great assemblage of fungi, and which, together with other factors, perhaps indicates the evolutionary trends in these forms.

Although several of the Homobasidiomycetidae have been reported to form conidia (Martens and Vandendries, 1933), no great diversity of conidial forms, such as is known in the Ascomycetes, occurs in the Homobasidiomycetidae. Oidia and arthrospores are produced by many species. How extensively asexual spores are formed in nature and how important a role they play in the life cycle of the higher Basidiomycetes, as a whole, are not known.

Classification. There are two more or less natural groups which can be distinguished within the Homobasidiomycetidae. These may be termed "series," since they have not been recognized as official taxonomic categories. They are the Hymenomycetes and the Gasteromycetes. The Hymenomycetes bear their basidia in a well-defined hymenium which becomes exposed while the basidiospores are still young and undeveloped. The Gasteromycetes, on the other hand, never expose their hymenial layer, which disintegrates at spore maturity. In some species of Gasteromycetes, the spores remain within the closed basidiocarp and are liberated only upon the breaking or weathering of the fruiting body; in other forms the spores are normally exposed, but such exposure is delayed until they are completely mature and the basidia have already disintegrated. In addition to the two great series there is a small but distinct group of Homobasidiomycetidae which produce no basidiocarps. They are parasitic on plants and produce their basidia in surface layers on the parasitized tissues of the host, in a manner similar to the Taphrinales. We place these fungi in the small but distinct order Exobasidiales.

The Homobasidiomycetidae are classified into many orders, their number varying with different authors. Following Martin (1961), we shall recognize eight orders in this book and shall discuss them rather briefly below to give you a general idea of the structure of these fungi.

SIMPLE KEY TO THE ORDERS OF THE SUB-CLASS HOMOBASIDIOMYCETIDAE

(Largely based on G. W. Martin, 1961)

- | | |
|--|--------------------------------|
| A. Basidiocarp lacking; hymenium covering the surface of the parasitized plant tissues | <i>Exobasidiales</i> |
| AA. Basidiocarp present, varying from an arachnoid subiculum to a very complex sporocarp | |
| B. Hymenium present and exposed before the spores are mature | Series
<i>Hymenomycetes</i> |

- | | |
|---|---------------------------------|
| C. Hymenium borne in various ways, but if basidia line pores or gills, texture of basidiocarp not soft and putrescent | <i>Polyporales</i> |
| CC. Hymenium borne on lamellae (gills), or if lining the interior of pores, then basidiocarp soft and putrescent | <i>Agaricales</i> |
| BB. Hymenium present or absent; basidiocarps remaining closed at least until the spores have been released from the basidia | Series
<i>Gasteromycetes</i> |
| D. Gleba fleshy to cartilaginous, or if slimy then not exposed at maturity | <i>Hymenogasterales</i> |
| DD. Gleba powdery, slimy, or waxy; if slimy, then exposed at maturity | |
| E. Glebal chambers usually not separating from the peridium or from each other ¹ | |
| F. Gleba powdery | |
| G. Hymenium present in early stages; spores mostly light colored, small | <i>Lycoperdales</i> |
| GG. Hymenium lacking or indistinct; spores mostly dark, large | <i>Sclerodermatales</i> |
| FF. Gleba slimy and fetid; exposed on a receptacle | <i>Phallales</i> |
| EE. Glebal chambers forming waxy peridioles, or entire gleba separating as a unit from the peridium | <i>Nidulariales</i> |

¹ In the family Arachniaceae of the Lycoperdales the minute, spherical glebal chambers remain intact and do separate.

order EXOBASIDIALES

The Exobasidiales is a small order of basidial fungi parasitic on flowering plants mostly belonging to the Ericaceae, but also on some species in the Empetraceae, Theaceae, Lauraceae, etc. (Savile, 1959). Several species are of economic importance, since, in addition to wild plants, they attack ornamental varieties of *Azalea*, *Rhododendron*, etc., and the leaves of the tea plant (Tubbs, 1947). Infection of the host often causes a swelling of the infected parts which is due chiefly to the hypertrophy of the host cells. The diseased tissues usually become red.

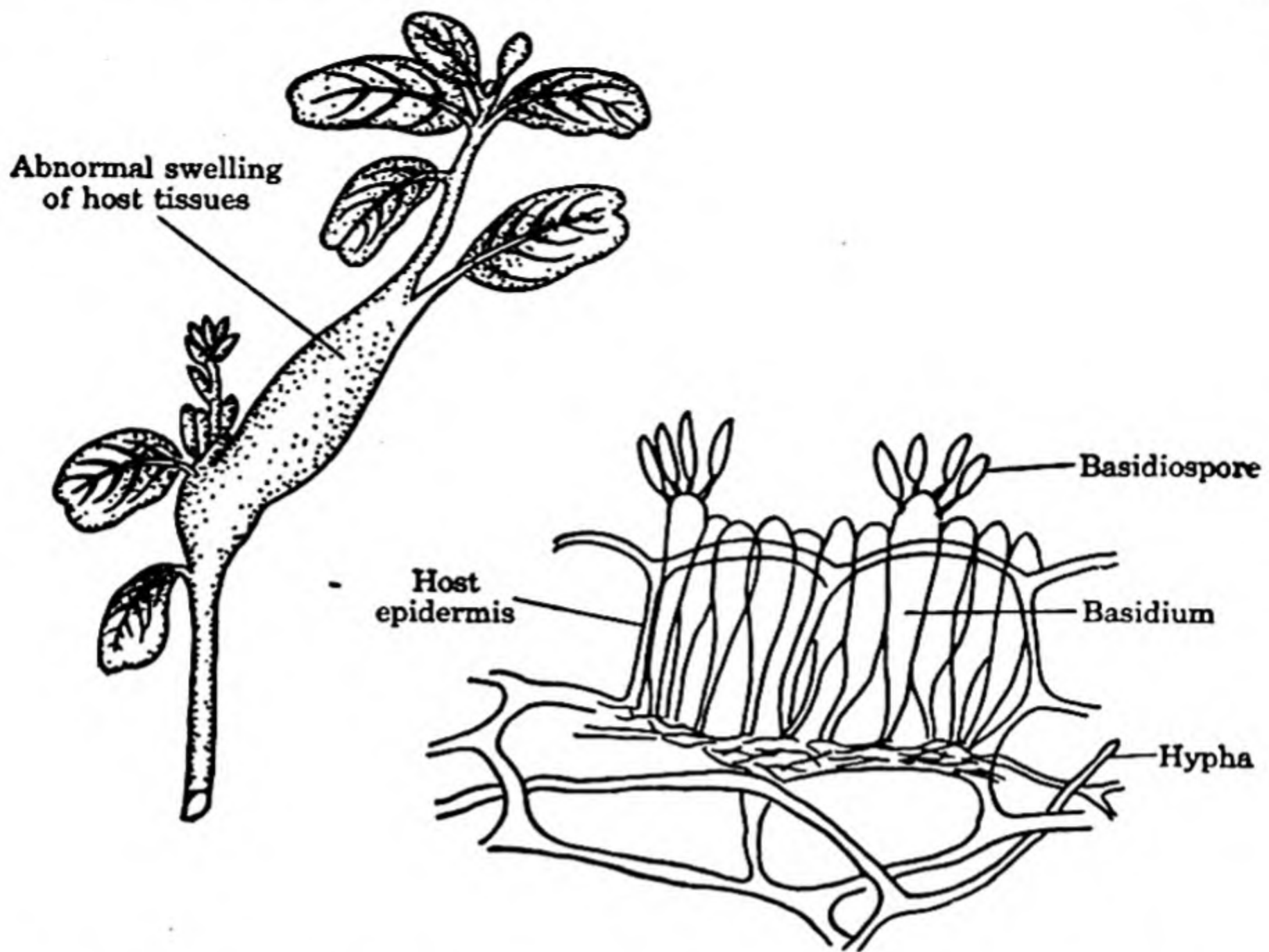


Figure 171. *Exobasidium vaccinii*. Redrawn from Woronin, in Rabenhorst's *Kryptogamen Flora*, 1884, Vol. I, E. Kummer, Leipzig.

All the Exobasidiales are placed in the single family Exobasidiaceae. The most commonly encountered genus is *Exobasidium* (Figure 171). The other genus in this family, *Kordyana*, is strictly tropical.

The basidia are formed directly from dikaryotic hyphae between the epidermal cells of the host, push through the cuticle, and form a layer on the surface of the host. Four, six, or eight basidiospores are produced, depending on nuclear behavior following karyogamy and meiosis in the basidium. The basidiospores are uninucleate. They germinate either by budding, producing blastospores, or by germ tube which infects the host and develops into a haploid primary mycelium. How the dikaryotic mycelium originates is not known, but Graafland (1960) has shown by single spore inoculations that *Exobasidium japonicum* on *Azalea* is homothallic.

The dikaryotic mycelium, devoid of clamp connections, is intercellular and feeds by means of haustoria. Several species have been grown in pure culture.

The relationships of this order are very obscure. Some authors

place the Exobasidiaceae in the Heterobasidiomycetidae. Others are firmly convinced that there is a relationship between *Exobasidium* and *Taphrina*. The similarities are striking, but the possibility of parallel evolution leading to similarity in morphology and physiology should not be disregarded.

series HYMENOMYCETES

Introduction. We generally classify all the Hymenomycetes in two large orders, the Polyporales and the Agaricales. The cantharelles, the coral fungi, the tooth fungi, and the pore fungi belong to the first; the mushrooms and the boletes, to the second. All produce their basidia on a more or less definite, orderly, hymenium layer, but the shape and size of the basidiocarp vary greatly, as does the manner in which the hymenium is borne.

Evolutionary Tendencies. In the forms considered most primitive, the basidiocarp is almost totally lacking, being represented by a weft of more or less loose hyphae which bear the basidia on the surface.

The first indication of an organized basidiocarp is a crust-like structure, flat on the substratum (resupinate) and having a smooth surface on which the hymenium is borne.

Both the basidiocarp and the hymenial surface may be greatly modified from this. The basidiocarp may be stipitate and pileate, that is, it may assume an umbrella- or shelf-like form with a smooth undersurface bearing basidia, or the hymenial surface may be wrinkled or toothed on a crust-like or pileate basidiocarp. In the toothed forms the teeth may be quite prominent, bearing basidia over their entire surface or only on a portion of their surface, and the entire basidiocarp may be branched and rebranched, assuming a coralloid form.

In another direction we find a crust-like basidiocarp with a pitted or porous surface, the hymenium lining the walls of the pores. Other basidiocarps are pileate and often corky or woody with a porous undersurface. The pores may be large and prominent, or so minute as to be virtually invisible to the unaided eye. The shape of the pores also varies from circular to hexagonal, to irregular, to elongated, to labyrinthine. In the last two forms it is difficult to distinguish between pores and lamellae (sing. lamella; L. *lamina*, dimin. form = plate). Lamellae, commonly called gills, are thought to represent the culmination of this series. The truly gilled fungi (mushrooms) are generally fleshy.

The Hymenomycetes have certain characters in common. They all expose their hymenia before the spores are mature. They bear their

usually apiculate spores perched obliquely on sterigmata and discharge them violently by the water drop method described earlier (page 434).

order POLYPORALES

As presently delimited, the Polyporales are Homobasidiomycetidae which bear their hymenia in various ways on definite, gymnocarpous¹ sporophores which, however, may be little more than subiculum-like webs of hyphae bearing basidia. The hymenium may be formed on one side of the sporophore (unilateral), or it may be formed on two sides or all around (amphigenous). It may be smooth, ridged, warted, or spiny, or it may line the inside of tubes or the surface of gills. If tubes or gills are present, the texture of the basidiocarp may be papery, leathery, or woody, but not soft and putrescent.

In his 1932 papers, Professor E. J. H. Corner of Cambridge University stressed the importance of hyphal structure of the basidiocarp in determining relationships and, therefore, in constructing a natural system of classification. In his monograph of the Clavariaceae (see page 499) Corner (1950) used the hyphal structure of the sporophores as his basic character in the first dichotomy of his phylogenetic key.

The order Polyporales is a very large and probably heterogeneous one. Whether the fungi included here constitute a related group of evolutionary series remains for future studies to elucidate. Many investigators are working on the morphology, physiology, cytology, and taxonomy of these fungi, and the classification system will continue to change until enough knowledge has accumulated to bring about a stabilized situation. We shall follow Martin's (1961) classification and recognize six families, which may be separated according to the following key:

SIMPLE KEY TO THE FAMILIES OF THE ORDER POLYPORALES

(Based on G. W. Martin, 1961)

- | | |
|---|------------------------|
| A. Hymenium smooth, roughened, or corrugated | |
| B. Basidiocarp typically cobwebby, membranous, leathery or hard | <i>Thelephoraceae</i> |
| BB. Basidiocarp usually pileate; generally fleshy, sometimes gelatinous | |
| C. Basidiocarp club- or coral-shaped, usually erect | <i>Clavariaceae</i> |
| CC. Basidiocarp mushroom-like or funnel-shaped | <i>Cantharellaceae</i> |

¹ With the hymenium exposed before the spores mature.

AA. Hymenium otherwise

D. Hymenium covering pendent warts, spines, or teeth

Hydnaceae

DD. Hymenium lining interior of pits or tubes

E. Pits shallow, fertile on ridges

Meruliaceae

EE. Tubes deep or, if shallow, sterile on ridges; texture not soft and putrescent

Polyporaceae

family THELEPHORACEAE

This family includes what are probably the most primitive forms of the Polyporales. The fruiting bodies are in many cases so thin as to resemble a coating of gray or pink paint on a fallen twig, as in the genera *Corticium* and *Tomentella*. Actually they can hardly be called anything more than thin layers of basidium-bearing hyphae. The more advanced members of this family, however, have definite, recognizable basidiocarps of papery, leathery, or woody consistency. The hymenium is unilateral. It is smooth, roughened, or wrinkled.

Among the species of economic importance are *Pellicularia filamentos* (= *Rhizoctonia solani*), which causes black scurf of potatoes; *Stereum hirsutum*, *Stereum gausapatum*, and *Stereum frustulatum* (Figure 172), all of which cause heart rot of oak, and the first of



Figure 172. *Stereum frustulatum*. From Kodachrome transparency, courtesy J. A. Herrick.

which also attacks a number of other important hosts, such as stone fruits and grape vines; and *Stereum purpureum*, which causes silver leaf disease of plum and other fruit trees and bushes. Some members of this family produce large basidiocarps, those of some species of *Sparassis* attaining a diameter of over a foot. Some of the larger members of this family are edible. *Sparassis radicata* is parasitic on conifers, causing a root and trunk disease. For many years, Burt's monograph (1914-1926) of the Thelephoraceae has been the chief taxonomic treatise for this family. Many genera are now being investigated in more detail, and some good modern monographs are being prepared. As more studies become available, the Thelephoraceae are being split into smaller families which are more homogeneous and which may represent individual evolutionary lines.

family CLAVARIACEAE

We usually place in the Clavariaceae those Homobasidiomycetidae whose club-shaped or branched, usually erect fruiting bodies bear a smooth or wrinkled hymenium on all sides. Nevertheless, as in many other families, the limits are difficult to define, for intermediate forms link this group with the Thelephoraceae, the Cantharellaceae, and the Polyporaceae.

Professor E. J. H. Corner in his excellent monograph (1950) of the clavarioid fungi emphasizes the hyphal structure of the basidiocarp as the chief indication of relationships in accordance with the principles he outlined in 1932. Presence and type of cystidia, type of branching, and color of spores are some of the other characters used in distinguishing among the many genera in this family.

The basidiocarp is composed of either one or two types of hyphae. It may be simple and more or less club-shaped, or it may be branched, sometimes intricately so. Apical branching may be radial or flattened, resulting in different types of basidiocarps. The hymenium covers the stem and branches on all sides, being absent only in the basal portion of the stem near the level or under the surface of the ground.

The Clavariaceae produce some of the most beautiful of fungal fruiting bodies. They are commonly called the coral fungi because the erect, intricately branched basidiocarps of some species resemble coral growth. The fruiting bodies of some are brilliantly colored in various shades of yellow, orange, violet, or other hues. Among the commonly encountered species are *Clavicornia pyxidata* (Figure 173) and *Ramaria stricta*. *Clavariadelphus pistillaris* is also fairly

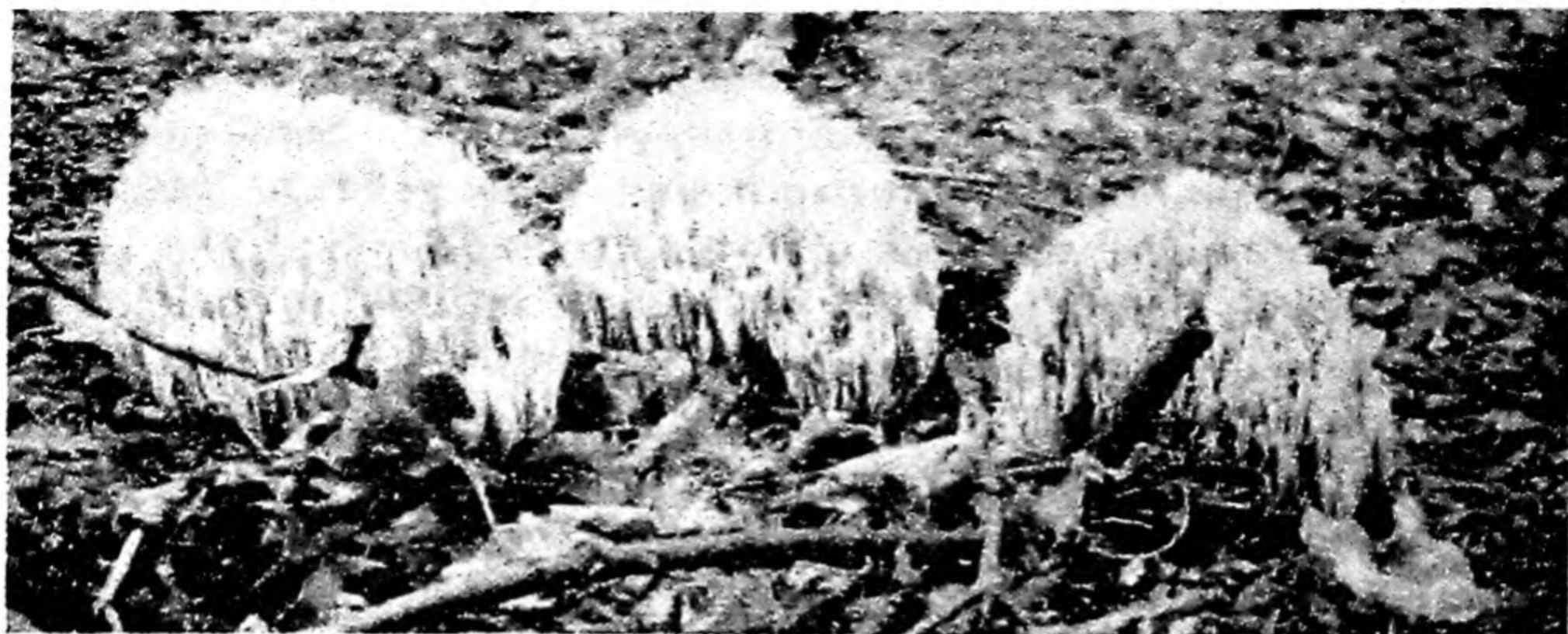


Figure 173. *Clavicornia pyxidata*. From Kodachrome transparency, courtesy F. C. Strong.

common in Europe and its variety *americanus* in North America. Many of the Clavariaceae, including this last species, are edible.

family CANTHARELLACEAE

This is a family of fungi which produce their hymenia on the underside of funnel-shaped or mushroom-like basidiocarps.

Two genera are usually included here: *Craterellus*, with thick, ridge-like folds, and *Cantharellus*, in which the ridges are very much like mushroom gills. *Craterellus* is sometimes placed in the Thelephoraceae and *Cantharellus* in the Agaricaceae, but it seems best to include them together in a separate family and recognize that they may represent intermediate forms. The famous European chanterelle (*Cantharellus cibarius*), also found in this country, is highly prized by those who appreciate the delectable aroma and exquisite taste of a fine mushroom (Figure 174).

family HYDNACEAE

The Hydaceae produce their basidia on spines or tooth-like projections which point downward. The basidiocarps of different species may resemble crusts, mushrooms, or coral. The coralloid fruiting bodies are generally softer and more gelatinous than those of the Clavariaceae, which tend to be tougher and more cartilaginous. *Hericium coralloides* (Figure 175) is a common species, producing beautiful, large, pure white, intricately branched fruiting bodies which



Figure 174. *Cantharellus cibarius*. Courtesy R. Pomerleau.



Figure 175. *Hericium coralloides*. From Kodachrome transparency, courtesy J. A. Herrick.

appear on tree stumps and in cavities of tree trunks. This easily recognizable species is edible. *Hericium erinaceus* and *Hericium laciniatum*, two species with large sporophores, are also edible. *Steccherinum septentrionale* is a serious parasite of maples, and *Echinodontium tinctorium* causes wood rot of conifers.

family MERULIACEAE

Formerly included in the Polyporaceae, this is another intermediate group which may link the Thelephoraceae with the Polyporaceae. The hymenium may be described as poroid. It is spread over shallow pits with fertile ridges and in some species is somewhat gelatinous.

family POLYPORACEAE

In the Polyporaceae, the basidia line the inner surface of pores or tubes (Figure 176). Here again the fruiting bodies may resemble crusts, shelves, or mushrooms. Among the first are various species of the genus *Poria* which are common wood rotters. The shelf-like polypores, sometimes known as bracket fungi, may be soft and pliable when young, but are generally tough, leathery, corky, or woody when mature. Some of the most common and most familiar fungi belong to this group. Many species of polypores cause diseases of forest and shade trees; others are important because they attack and destroy lumber. Indeed, this family, probably more than any other, is re-

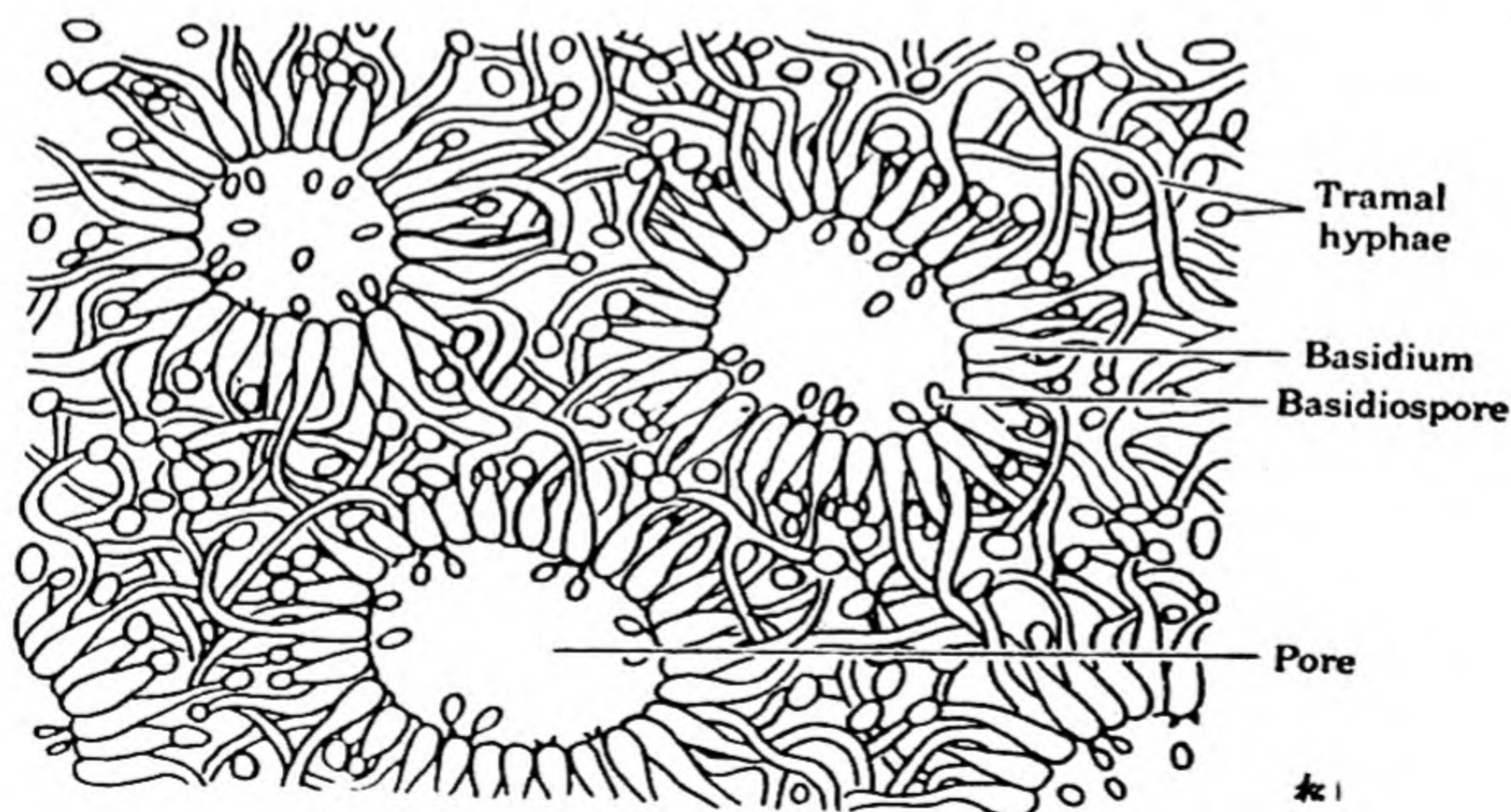


Figure 176. Hymenium of a polypore.



Figure 177. *Polyporus sulphureus*. From Kodachrome transparency, courtesy F. C. Strong.

sponsible for most of the wood rot against which wood preservatives are employed, at a cost of large sums of money to industry.

The most common genera of this family,¹ in addition to the aforementioned *Poria*, are *Polyporus*, *Fomes*, and *Ganoderma*. The fruiting bodies of *Polyporus* are annual; those of *Fomes* are perennial, growing and increasing in size year after year. Some of the economically important and commonly found species in these genera are *Polyporus sulphureus* (Figure 177), the sulfur mushroom, which causes wood rot of oaks and other trees, and whose large fruiting bodies are sulfur-yellow; *Polyporus squamosus*, which causes a serious heart rot of a number of hosts in Europe and America; *Polyporus versicolor*, a widely spread wood rotter with a zonately marked pileus; and *Polyporus cinnabarinus*, easily recognized by its cinnabar-red, corky fruiting bodies. The basidiocarps of *Fomes* may generally be recognized by the extremely minute pores, which can hardly be seen without the aid of a lens, and by their woody texture. Small at first, these perennial fruiting bodies attain large size in many species. *Fomes applanatus* is one of the most common shelf fungi (Figure 178). The pure white, smooth, flat undersurface invites the pen or brush of the amateur artist much as the freshly painted, white wall irresistibly draws the pencil of a small child. This species attacks the dead wood of beech and many other species of hardwood trees. The heavy, hoof-

¹ For the most part I am using here the generic names in Overholts (1953).



Figure 178. *Fomes applanatus*. From Kodachrome transparency by the author.

like fructifications of *Fomes igniarius* are known to live 80 years or more. An interesting species is *Ganoderma lucidum*, which produces reddish brown fruiting bodies whose lateral stem and upper surface are coated with a hard, shiny substance resembling sealing wax.

Among the woody, shelf-like polypores, two genera, *Lenzites* and *Daedalea*, are of especial interest morphologically and taxonomically. *Lenzites* has elongated pores which approach a gill-like structure. To such an extent is this true that many keys to the higher Basidiomycetes include this genus under both the Polyporaceae and the Agaricaceae. In *Daedalea*, this tendency is even more exaggerated, with the pores not only elongated but labyrinthine as well. These two genera may be indicative of an evolutionary tendency in the development of the hymenium from poroid to lamelloid.

Irpex, a genus with flat, crust-like sporophores, is commonly found on rotting wood. The sporophore has a porous surface, the walls of the pores extending irregularly like teeth. *Irpex* is, therefore, intermediate in appearance between the Hydnaceae and the Polyporaceae.

order AGARICALES

The large order Agaricales includes the fungi whose fruiting bodies we commonly call mushrooms or toadstools. Ordinarily we call the edible species mushrooms and the poisonous ones toadstools. Mor-

phologically, the two groups as a whole are indistinguishable, closely related species of the same genus often differing in chemical composition, one being perfectly safe, the other containing poisonous substances. Another group of fleshy, large fungi which belong here are the boletes.

The mushrooms bear their basidia on the surface of gills or plates (lamellae) which are generally produced on the underside of usually fleshy, sometimes tough, umbrella-like sporophores. The gills are usually not readily separable from the rest of the basidiocarp. In the boletes, the basidia line the inside of deep tubes or, more rarely, shallow pits, on the underside of soft and putrescent mushroom-like sporophores. The layer of tubes is, in most species of boletes, readily separable from the basidiocarp.

The Agaricales have probably been studied to a greater extent than have any of the other orders of the Homobasidiomycetidae, and a voluminous technical literature has accumulated. Because many people hunt mushrooms for food, mycologists have also written many popular and semi-popular books dealing with the identification of the common edible and poisonous species. The titles of some of these are listed at the end of this chapter.

Occurrence, and Importance to Man. The Agaricales, as an order, can be said to be cosmopolitan. They have been known to man ever since he became aware of his environment, and they are among the relatively few fungi which, therefore, have common names in addition to scientific binominals. You will remember that the word *mykes*, from which mycology is derived, actually meant mushroom to the ancient Greeks, and thus, etymologically, mycology is the study of mushrooms.

Many species are found in widely separated geographical areas. In habitat, the Agaricales vary considerably, some species being restricted more or less to certain substrata. Thus, *Agaricus campestris*, the common field mushroom, grows in open fields. *Agaricus rodmani* (Rodman's mushroom) (Figure 179) is an urban inhabitant, found on city lawns and very frequently next to the curb on city streets. *Marasmius oreades*, the fairy ring mushroom, is also common on city lawns, forming rings of mushrooms on the grass. Some species prefer wooded areas: *Collybia longipes*, the long-rooted mushroom, is generally found on the ground in moist woods; *Collybia velutipes*, the velvet-stemmed *Collybia*, grows on dead wood—logs or cut lumber—from spring to late fall.

Various species of agarics produce their fruiting bodies at different



Figure 179. *Agaricus rodmani*. From Kodachrome transparency by the author.

seasons of the year. Some are early spring mushrooms, disappearing by the time summer arrives. One of the earliest is *Pholiota praecox*. On the other hand, *Pholiota autumnalis* and *Pholiota adiposa* are fall agarics. In general, fall is probably the best season of the year for hunting mushrooms, at least in the north temperate zone.

Economically, the Agaricales are of considerable importance. Their significance as mycorrhizal fungi is not too well established, but a number of them are known to form mycorrhizae with trees. Many species are important as wood destroyers. *Armillariella mellea*, the honey mushroom, causes root rot of apple and many forest trees.

Much research is being devoted to an examination of a large number of species of the Agaricales for their possible use in the production of antibiotics. Although no startling discoveries have been made as yet in this field, these fungi do produce antibiotics and it is possible that by the time all the common species have been investigated, some new and useful substance may be discovered.

A great industry has been developed in the United States and Europe, based on the cultivation of *Agaricus campestris bisporus*¹ on a large scale in the western world. The cultivation of the *Shii-*

¹ Also called *Agaricus bisporus* and *Agaricus hortensis*.

Take mushroom (*Cortinellus berkeleyanus*) is expanding in Japan and has reached considerable proportions.

Finally, the hallucinogenic mushrooms, about which we shall say more on page 519, are being used experimentally in medicine as an aid to psychotherapy.

Edible and Poisonous Mushrooms. A discussion of the Agaricales should include a word about their use as food. Mushrooms have some value for their protein and vitamin contents, but not too much of a case can be built for them on this point. People who like to eat them do so for their flavor and need no other inducement. Those who do not like mushrooms miss nothing, so far as food value is concerned, that cannot readily be obtained from other foods. The fact that a great mushroom-growing industry has developed and is constantly growing in the United States is proof that a great many people appreciate the agarics as food. Mushroom lovers who make it a hobby to learn the wild species and hunt them for food have an additional gastronomic pleasure in the variety of flavors they find, besides the fun of roaming the forests and fields after their prize.

The question which the prospective mushroom hunter will first ask is: "How can I distinguish between edible and poisonous species?" The only correct answer to this question is that there is no known test to which you can subject an unknown mushroom specimen to learn whether it is edible or not. Dr. J. A. Herrick of Kent State University published (1948) a very interesting article on this question. He brought together various dangerous superstitious "rules" which supposedly distinguish between edible and poisonous mushrooms. Among them are the blackening of silver, the blackening of onions, the peeling of the cap, and the color of the gills. All these "rules" are worthless, as Herrick points out, and the only safe course is to learn to recognize individual species. You can learn to identify some of the more common species by the use of a good manual and a lot of practice. There are many good manuals available to help you identify mushrooms, and some of them are well illustrated with excellent photographs. The epitome of mushroom manuals was reached in 1949, when Dr. A. H. Smith of the University of Michigan, an eminent student of the agarics, published his *Mushrooms in Their Natural Habitats*, illustrated with 231 stereophotographs in natural color. Regardless of the manual you use, however, as a beginner you will do well to have your identifications checked by a professional mycologist and preferably a specialist in the taxonomy of the Agaricales. The pitfalls are many, and you can make a serious mistake but once!

Somatic Structures. In observing and studying sporophores of fungi as large as those of most Agaricales, the student is likely to forget that the mushroom is not the whole fungus; on the contrary, the mycelium which covers a much greater area is in fact the body of the organism.

The mycelium of the Agaricales, as well as that of the Polyporales, is typically basidiomycetous, in that it arises as primary mycelium from a uninucleate spore, becomes binucleate as a result of hyphal fusion or oidization (union of an oidium with a somatic hypha), and eventually, as tertiary mycelium, forms complex tissues—the mushrooms—which produce basidia. The uninucleate mycelium is of short duration in nature, the binucleate mycelium being the more abundant, perennating, and producing mushrooms year after year.

Mushroom mycelium, which normally inhabits the ground, has a tendency to grow in all directions from a central point and to form a large, invisible circular colony. When the time for sporulation arrives, the sporophores are produced at the tips of the hyphae and thus form a ring. Such a ring has been called a fairy ring because of an old superstition that mushrooms growing in a circle represent the path of dancing fairies. Fairy rings are particularly evident in grassy fields or on city lawns, and may be either arcs or complete circles. *Marasmius oreades*, the fairy ring mushroom, is the best known of a number of Basidiomycetes which form rings. *Lepiota molybdites*, Morgan's mushroom, is another species. Inside the circle of mushrooms which characterizes the fairy ring, and concentric with it, there is a distinct zone of grass which is noticeably greener than the grass elsewhere in the vicinity. The greener color is due to the nitrogenous substances which become available to the grass as the older hyphae of the fungous mycelium die. According to Butler and Jones (1949), the perennial mycelium of *Marasmius oreades* is known to live for as many as 400 years and produce a crop of mushrooms every year.

The secondary mycelium of the Agaricales, which gives rise to the fruiting bodies, may or may not possess clamp connections. Some of the Agaricales produce greatly compacted masses of hyphal strands, covered by a cortex. These are rigid structures attaining great length in which the hyphae have lost their individuality, and the entire strand acts as a unit. Such are the black, brittle rhizomorphs of *Armillariella mellea*, which may often be found forming a rigid network under the bark of trees.

An interesting phenomenon of the mycelium of a number of agarics is bioluminescence. Organic matter—generally pieces of decaying

wood—penetrated by the mycelium of a bioluminescent fungus will glow in the dark. This phenomenon is commonly called fox-fire. Fungal luminescence is easily demonstrable in the laboratory either by bringing in wood completely penetrated by the mycelium of *Armillariella mellea*, or by preparing mycelial cultures of this or some other agaric which shows this effect. The phenomenon is briefly discussed by Cochrane (1958), who lists a number of references for a more detailed discussion.

The physiology of growth of the Agaricales has been studied extensively, and the growth requirements of a large number of species are fairly well known. The standard references on the physiology of fungi should be consulted for this phase of the subject. Some of the most recent papers are by Robbins (1950), Yusef (1953), N. Fries (1950, 1954), L. Fries (1955), and Denyer (1960).

Asexual Reproduction. Although several species in the Polyporales produce conidia, few of the Agaricales have been shown to have a distinct asexual phase. A number of species (*Coprinus fimetarius*, *Coprinus lagopus*, *Collybia conigena*, etc.) produce oidia. These oidia perform a dual function in some species: they may either germinate, giving rise to mycelium, or behave as spermatia, uniting with hyphae of the opposite strain. Some species, such as *Agaricus campestris*, produce chlamydospores.

Sexual Reproduction. Sexual reproduction takes place by means of hyphal fusion (somatogamy) or oidization. Homothallism is rather rare in the higher Basidiomycetes. The great majority of species which have been investigated are heterothallic bipolar or tetrapolar. This holds true for the Agaricales as a whole as well as for the Polyporales. For excellent summaries of our present knowledge of the sexuality in the Basidiomycetes read the papers by Whitehouse (1949*a, b*) and by Raper (1953–1960) listed at the end of this chapter.

The Basidiocarp. The basidiocarp of most Agaricales is the well-known mushroom. Beginning as a tiny knot of hyphal cells, it eventually develops into a small, globose, or ovoid body commonly called the button stage. If you cut a mushroom button longitudinally, you will see that the gills are already forming. In some species the margin of the young pileus is connected to the stem by a membrane, technically known as the inner veil. As the basidiocarp grows (and growth can be very rapid), the upper portion of the button expands into the cap or pileus and the inner veil tears. As the inner veil tears, it often becomes severed from the margin of the pileus and

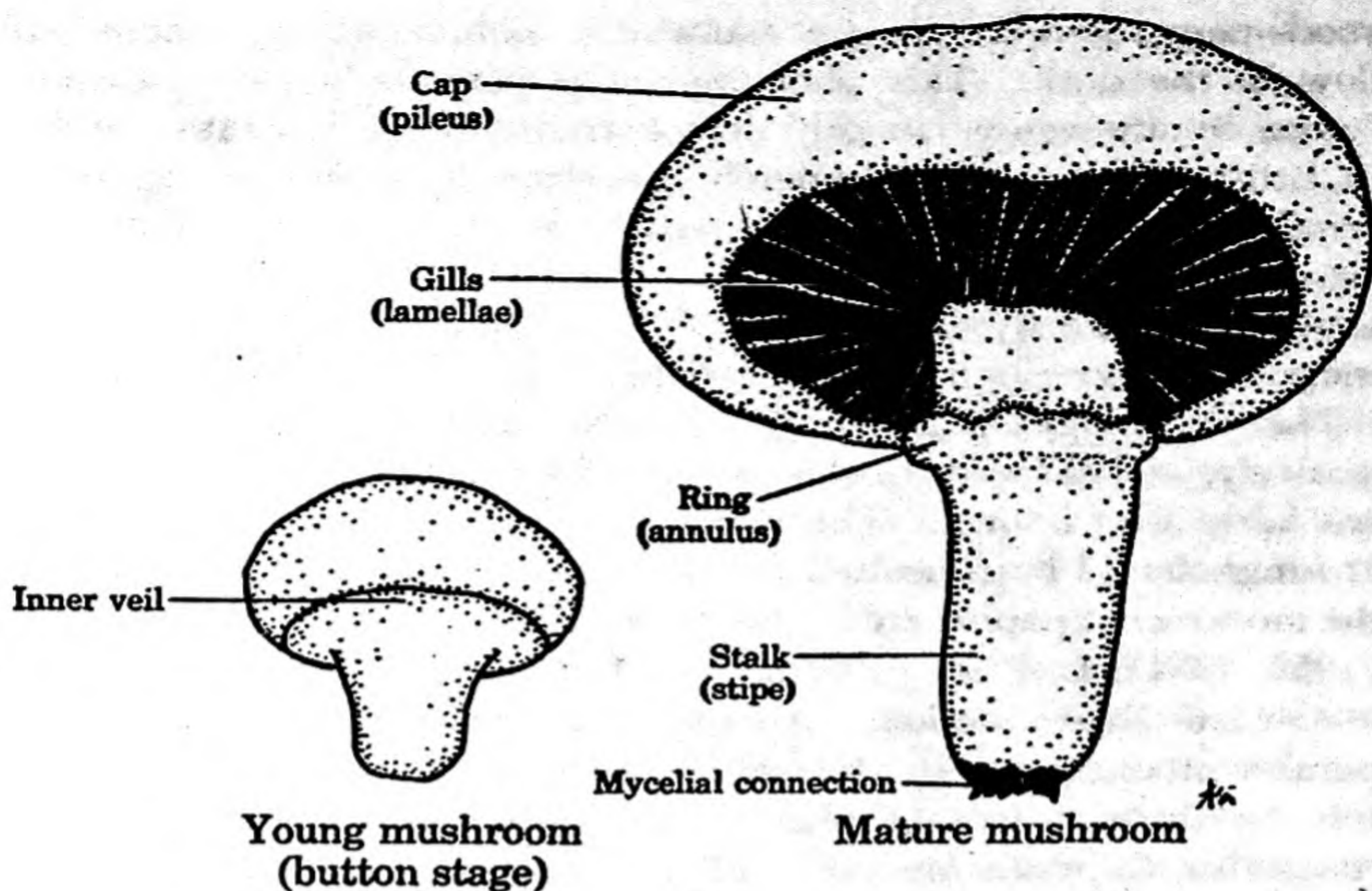


Figure 180. Basidiocarp of the Agaricaceae (*Agaricus* type).

remains attached to the stem in the form of a ring or annulus (pl. annuli; L. *annulus* = ring) (Figure 180). In certain mushrooms whose development is somewhat different from that described above, as the inner veil tears, portions of it hang down from the cap like a thin, cobwebby curtain, the *cortina* (pl. *cortinae*; L. *cortina* = curtain). In still another type of development, characteristic of *Amanita* and some other genera, the young button is entirely covered by a universal veil. When the sporophore enlarges and the pileus finally expands, the universal veil tears in such a manner as to leave a cup-shaped body, the *volva* (pl. *volvae*; L. *volva* = covering) around the often bulbous base of the stem. The remnants of that part of the universal veil which covers the pileus can be seen in the form of scales on the cap (Figure 181). These various structures (volva, annulus, cortina, scales) are important in the classification of the genera of the Agaricales. Because in many cases they are quickly evanescent, they make identification difficult for the beginner.

The lamellae or gills of the basidiocarp hang below the pileus in the form of thin, narrow, or wide strips of tissue radiating from the margin toward the stalk. In many species the inner edge of the gills is attached to the stalk and may run down the stalk for a distance.

The position of the inner edge of the gills, with reference to the stalk, is a valuable character in identifying genera and species.

The inner tissue of the gill, called the *trama* (L. *trama* = woot), consists of plectenchymatous tissue usually made up of elongated cells. The trama of the genera *Russula* and *Lactarius* characteristically contains groups of large, globose or oval cells (sphaerocysts) scattered among the elongated cells (Figure 182B). Chiefly on this basis we remove these two genera from the Agaricaceae and place them in the family Russulaceae. On the surface of the trama, covering both sides of the gill and often the edge as well, is the hymenium, a closely packed layer of basidia interspersed with paraphyses or cystidia or both in some species (Figure 148). In *Coprinus* the cystidia are long enough to extend from one gill to the next, keeping the gills apart. Each basidium usually bears four spores which are forcibly shot off and then fall below the pileus under the influence of gravity. In still air, they become deposited below the pileus in a mass, forming a spore print.

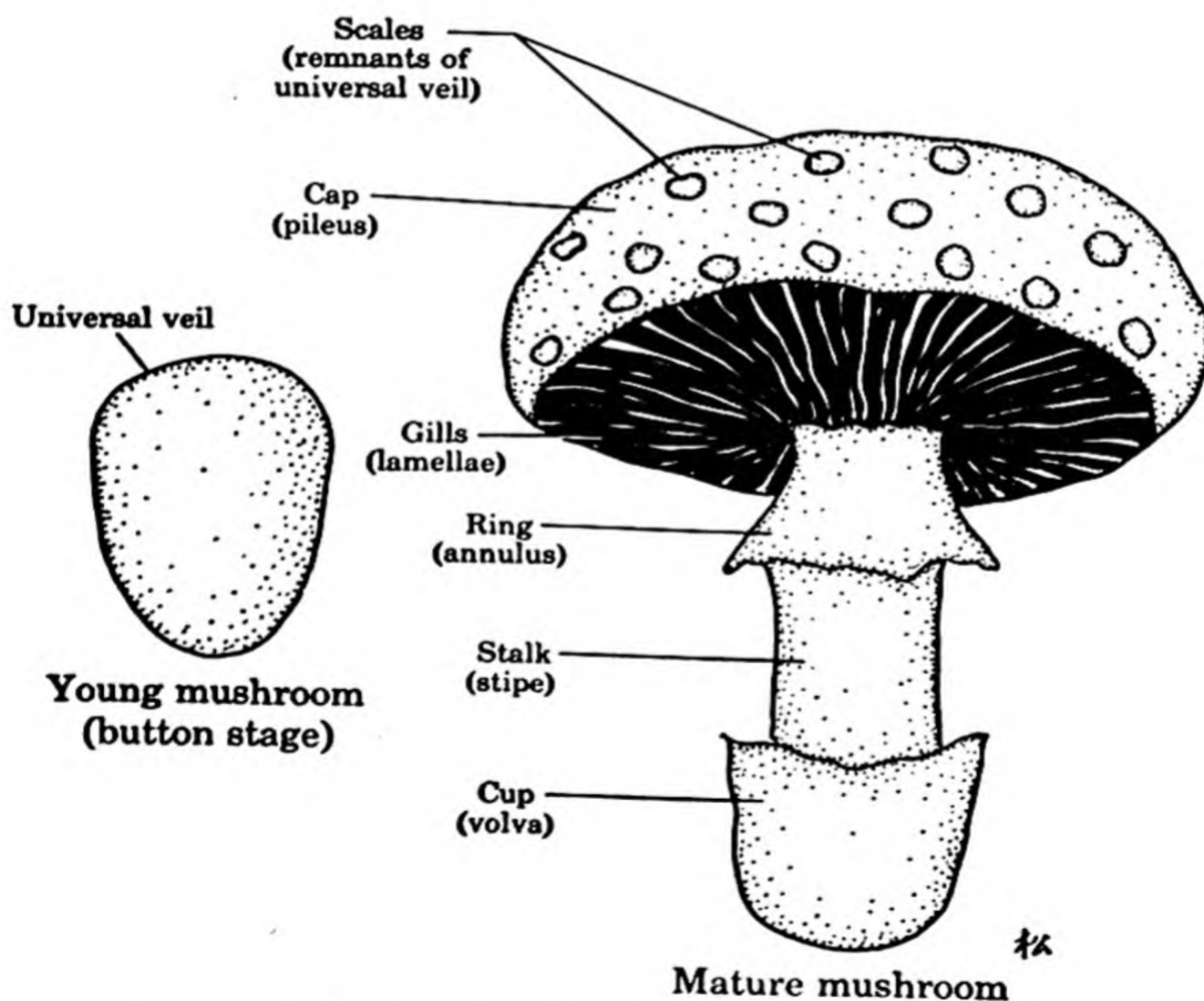


Figure 181. Basidiocarp of the Agaricaceae (*Amanita* type).

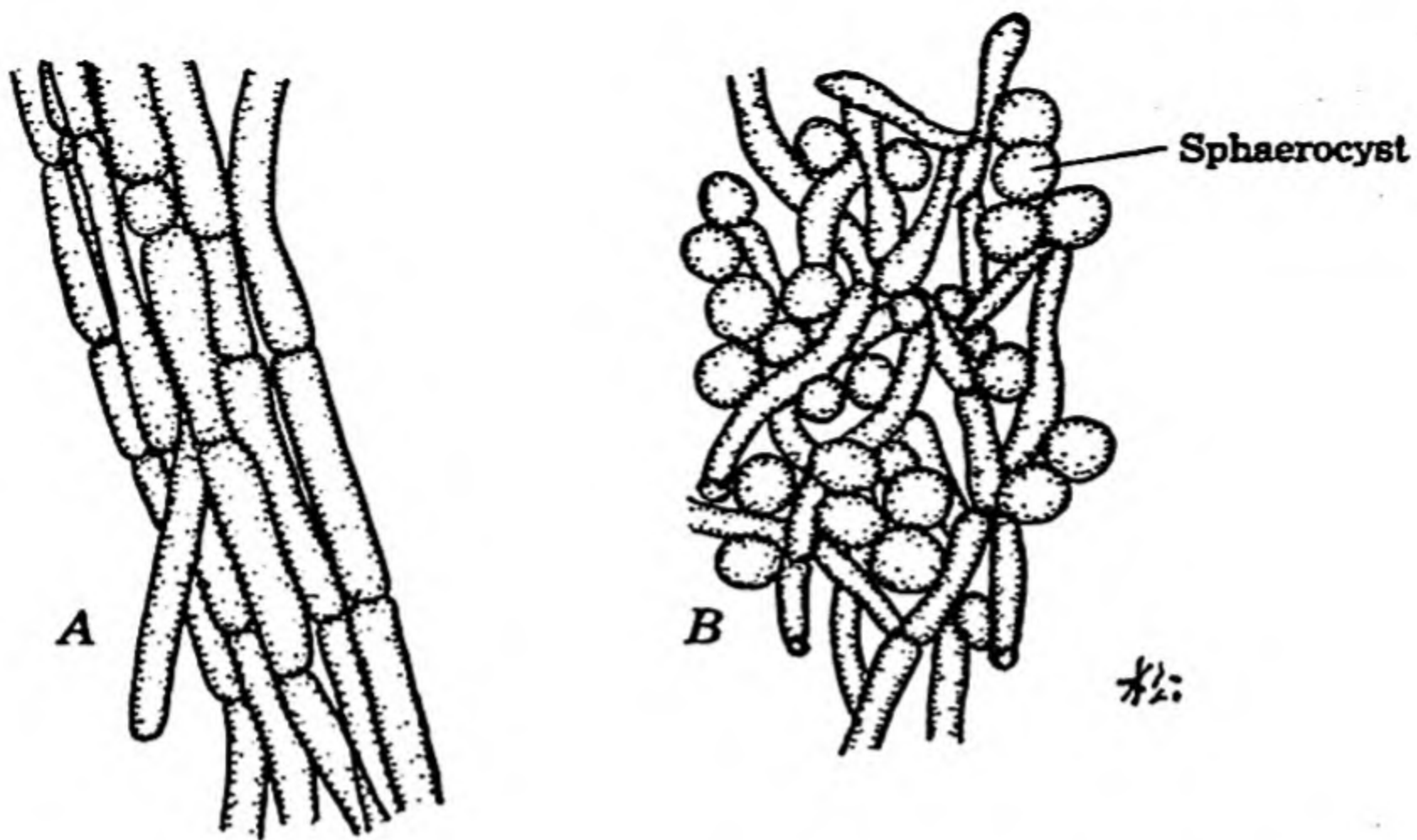


Figure 182. Two types of trama. A. Without sphaerocysts. B. With sphaerocysts.

The Spores. In as large a group as the Agaricales you would expect to find a great variation in the characters of the spores. A perusal of Section XIII (pp. 63–75) on spores, in Singer's treatise (1949), "The 'Agaricales' (Mushrooms) in Modern Taxonomy," will convince you of the validity of this expectation. In shape, the spores vary from globose to elongated; in length, from 2 to 40 μ ; in color, from colorless to black. In some spores, the wall consists of five layers, the chemical composition of which is not well known. Many spores give an amyloid reaction with iodine, and this test is being used increasingly in the classification of the Agaricales, as is the amyloid reaction of the ascus, an established test in the classification of the Ascomycetes. The external ornamentation of the spore wall is also a useful criterion of possible relationships. Singer recognizes no fewer than twelve types of ornamentation of the outermost spore layer (perisporial ornamentation).

Classification. A much more thorough understanding of the morphology of the basidiocarp, of the hymenial elements, and of the spores than you can get from the very brief discussion above is a necessary prerequisite for a high-level discussion of classification. If you have a particular interest in the Agaricales, therefore, you should study carefully the General Introduction (109 pages) of Singer's treatise (1949) as well as that in Smith's (1949) *Mushrooms in Their Natural Habitats*.

The order Agaricales, although very large, appears to be a much

more homogeneous and natural group than the Polyporales as now delimited. As we study the Agaricales, certain evolutionary lines become evident which enable us to separate them into natural families. As yet, research has not proceeded to the point where all the families that have been proposed may be unhesitatingly accepted by all. In the older system, on which many time-honored monographs are based, all the Agaricales were included in one family—the Agaricaceae.

One classification of the Agaricaceae which attempts an arrangement on a more natural basis is that of Dr. Rolf Singer. Singer (1949) arranged the genera which had previously been included in the Agaricaceae and the Boletaceae into no fewer than fifteen families, and used a few chemical as well as morphological characteristics for the separation of the families and genera. Again we shall follow the more conservative viewpoint of G. W. Martin (1961) and discuss the Agaricales under five families, recognizing that eventually a great number may be segregated out of the Agaricaceae, which still remains the largest of the five.

KEY TO THE FAMILIES OF THE ORDER AGARICALES

(Based on G. W. Martin, 1961)

- A. Basidiocarp soft and putrescent; hymenophore usually separating readily from context
 - B. Hymenophore consisting of tubes, sometimes of shallow pits *Boletaceae*
 - BB. Hymenophore consisting of lamellae (gills), which are often united by conspicuous veins *Paxillaceae*
- AA. Basidiocarp fleshy to tough or membranous; hymenophore not separating readily from context
 - C. Context of the sporophore containing nests of sphaerocysts *Russulaceae*
 - CC. Sphaerocysts absent
 - D. Gills waxy, broadly triangular in section *Hygrophoraceae*
 - DD. Gills not waxy, narrow in section *Agaricaceae*

We shall discuss three of the above families very briefly.

family BOLETACEAE

The Boletaceae constitute a family which, in its wider sense, is more or less easily distinguished from most other Agaricales by the tubular character of the hymenophore. The tubes are usually of

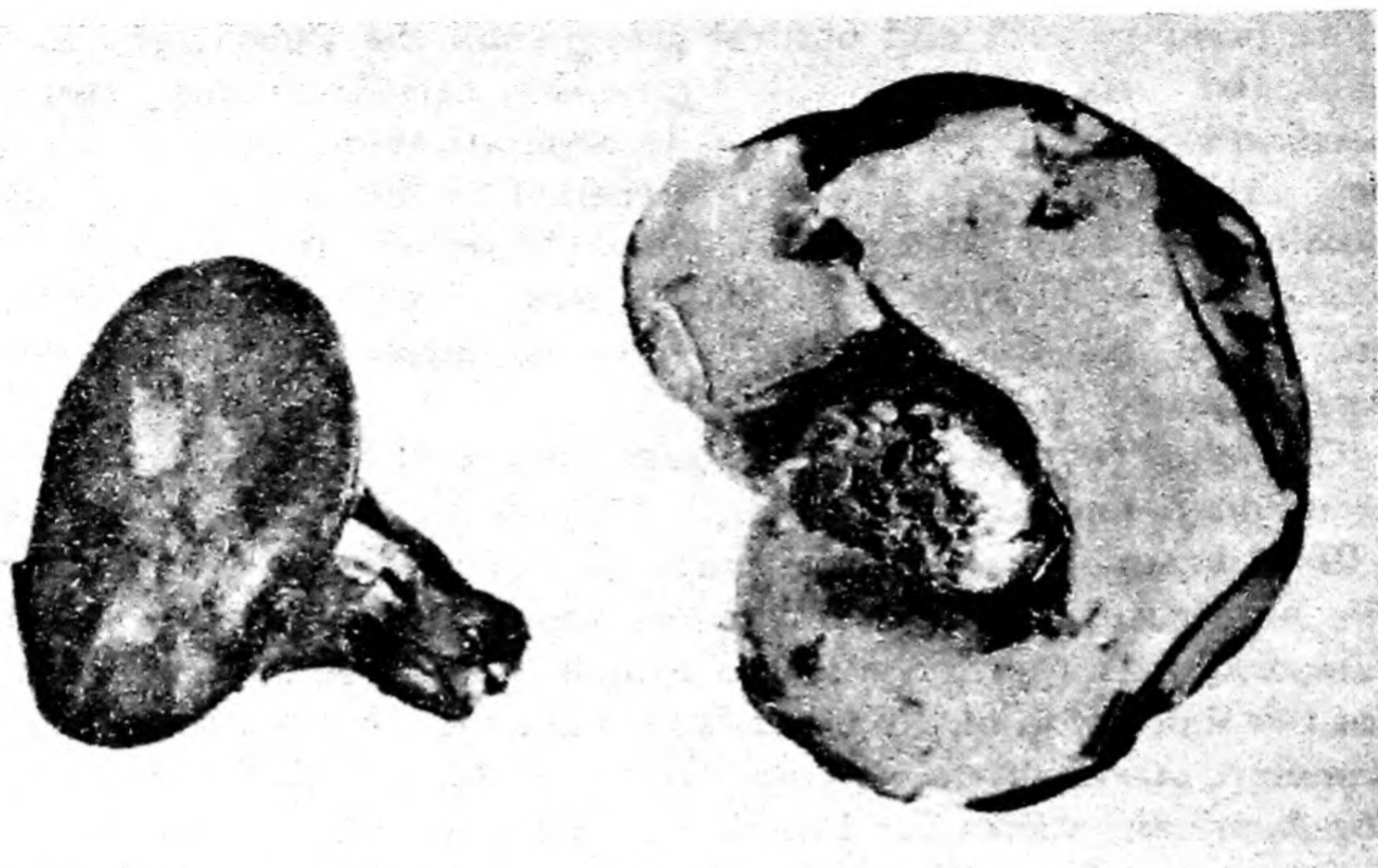


Figure 183. *Paragyrodon sphaerosporus*. From Kodachrome transparency, courtesy F. C. Strong.

equal length and may easily be stripped from the context of the basidiocarp in most species. This is not the case with species of *Boletinus* or *Strobilomyces*.

The Boletaceae are world-wide in their distribution, occurring wherever the rainfall is adequate for the development of most mushrooms.

The fruiting bodies of most species are fleshy and soft (Figure 183). They decay easily and quickly. The mycelium grows in the ground and that of many species forms mycorrhizae with pine, larch, birch, sassafras, etc. This explains why the fruiting bodies of some species occur only in association with certain trees.

Most species appear to be edible, but some are bitter or acrid and a few may be poisonous. *Boletus edulis* is widely used in Europe as food. The dried pulverized sporophore is sold in packets in Switzerland and elsewhere to flavor soup. Nevertheless, according to Bessey (1950), it contains a substance which when injected into the bloodstream is extremely poisonous but which is destroyed during digestion when the fungus is eaten. The same species was shown (Lucas *et al.*, 1957) to contain another substance which inhibits tumor growth in experimental animals.

Coker and Beers (1943) recognize three genera of Boletaceae:

Boletus, *Boletinus*, and *Strobilomyces*. Singer (1949), on the other hand, splits the family into the Boletaceae with fifteen genera and the Strobilomycetaceae with three.

family RUSSULACEAE

The Russulaceae are easily distinguished from all other families of the Agaricales by the presence of sphaerocysts in the context of the pileus and often in the trama of the gills. The family includes two genera: *Russula* and *Lactarius*.

Members of the genus *Russula* are easily recognized. All parts of the mushroom, particularly the gills, are generally very brittle. The stalks are often short and thick and the caps quite often colored, sometimes brilliantly. The genus is a very large and difficult one, and the identification of species is a task for the specialist. A beautiful, but probably poisonous, species is *Russula emetica*. It has a very sticky, brilliant red cap (the color of which, however, may vary through pink to white) and a short, thick, pure white, brittle stem; it grows commonly in sphagnum bogs and may be quite abundant.

The sporophores of *Lactarius* exude a watery or milky juice if cut when fresh. This juice flows in a system of lactiferous tubes which ramify throughout the tissues of the sporophore. The latex may be colorless or colored, creamy, yellow, blue, or red. In some species the color changes after the milk has been exposed for some time, and this change is important in identifying species. Only fresh specimens should, therefore, be used for identification. The genus is a very large one with over forty species (Kauffman, 1918). The peppery *Lactarius* (*Lactarius piperatus*) is one of the most commonly encountered late summer-early fall species. The cap often exceeds 6 inches in diameter. With age its edges turn up and the mushroom assumes the shape of a funnel. The intensely peppery taste characteristic of this species disappears when the mushroom is cooked.

family AGARICACEAE

The Agaricaceae, as we limit the family here, include the majority of mushrooms. The Agaricaceae bear their basidia on gills which are neither waxy nor easily separable from the context of the pileus. The gills are narrow in section. Sphaerocysts are absent from both the trama of the gills and the context of the pileus, but cells larger than usual are sometimes present in these tissues.

As mentioned earlier, Singer splits the Agaricaceae into many families on a number of characters, but much monographic work remains to be done before the limits of these families are well established.

Classification. For convenience, the Agaricaceae are generally subdivided artificially into five groups on the basis of the color of their spores. The five color categories recognized for the spores are white, pink, brown (ochre), purple, and black. Unfortunately, it is not always easy to place a given mushroom in its proper group because of intermediate colors which require interpretation in accordance with the fixed categories. Furthermore, the "white-spored" group usually includes some species which yield cream or yellow spore prints and some with unmistakably green spore prints. The color of the spores is determined by making a spore print from the sporophore to be identified. The stem is cut off squarely with the edge of the gills and the pileus is placed gills down, so that half of it rests on a piece of white paper and half on a piece of dark paper. The pileus is then covered with a bell jar or similar cover to prevent it from drying out too quickly. After a few hours, the pileus is lifted and the mass of spores, which meanwhile has been deposited on the two pieces of paper in the form of a spore print, is examined and the color of the spores is determined.

Here are a few of the white-spored agarics which you can learn to recognize. *Schizophyllum commune* is one of the most common species. World-wide in its distribution, easy to recognize and to cultivate, this species has been used extensively for the study of heredity and nuclear behavior and a large number of researches based on this organism have been published. The gray, fan-shaped sporophores are usually small, ranging from less than $\frac{1}{2}$ inch to about $1\frac{1}{2}$ inches in diameter. They are laterally attached to decaying logs, branches, or sticks. No stalks are present. The chief distinguishing feature is the character of the gills, which radiate out from the point of attachment. They are thick, and their edges are split, the split often being very shallow, in the form of a groove. *Armillariella mellea*, the honey mushroom, generally grows in clusters around the roots of trees or dead stumps in the woods. It is honey-colored and has a somewhat thickened base and a prominent ring when young. The color, however, may vary and the ring disappears with age. This species is edible and plentiful. *Collybia longipes* has an almost flat, tan cap and pure white gills. It has a long, slender stem above the ground, which is prolonged below the



Figure 184. *Pleurotus sapidus*. From Ansco color transparency by the author.

ground into a structure several inches long which resembles a tap root. *Collybia velutipes* is a comparatively small mushroom which generally grows in dense clusters on logs or tree stumps. It has a reddish orange cap, which is very sticky when wet, white gills, and a brown velvety stem. Both these species are edible, but are not of the finest flavor. The oyster-mushroom, *Pleurotus ostreatus*, and its relative, *Pleurotus sapidus*, both edible and of excellent flavor, grow on logs or tree stumps in shelf-like layers (Figure 184). They have a very short, lateral stalk and an oyster-shaped pileus. *Pleurotus ulmarius*, also good to eat, is a large white mushroom with a thick, almost central stalk. It grows on living elm trees or on elm logs.

The various species of *Amanita* (Figure 185), many of which are highly poisonous, are also white-spored. They have both a volva and a ring, although the ring of some specimens disappears early and the volva may be somewhat buried and hard to see.

Amanita muscaria, called fly-mushroom (Figure 185) because of its former use as an insecticide, is cosmopolitan and not infrequently encountered. There are a number of color variations the taxonomic significance of which has not been determined. Yellow, orange, or brilliant red caps speckled with cream or white flakes make this mushroom spectacular, especially since, in some specimens, the cap



Figure 185. *Amanita muscaria*. From Kodachrome transparency, courtesy J. A. Herrick.

exceeds 5 inches in diameter. Much has been written about the properties of this mushroom and its use in orgiastic festivals of certain Siberian tribes (Taylor, 1949). The mushroom is variously classified: as edible, if the veil is peeled off; as hallucinogenic, if eaten in small quantities; as poisonous; and as deadly. There is no doubt that it contains a toxic substance, muscarin, which can cause death in man and animals if consumed in quantity. Atropin is administered as an antidote for the toxin of this species.

Amanita verna, the destroying angel, is the deadliest of all mushrooms known. This pure white species may be found throughout the summer and early fall in woodlands. *Amanita phalloides*, a very poisonous species, is a European mushroom. Whether it also occurs in America is doubtful. *Amanita brunnescens* is also deadly. No antidotes are known for the toxins of the last three species.

In the pink-spored group, *Pluteus cervinus*, an edible species, is one of the most common. *Clitopilus abortivus*, many of whose sporophores become aborted and never mature, is another common pink-spored agaric which, according to McIlvaine (1900), is edible.

In the ochre- or brown-spored group, the various species of *Pholiota* are probably the most commonly encountered. *Pholiota praecox* is one of the earliest mushrooms to appear in the spring, growing in grassy, open places. It is edible but has little flavor. *Pholiota adiposa*, *Pholiota squarrosa*, and *Pholiota squarrosoidipora* are all

autumn species. The genus *Psilocybe* in the brown-spored group is of great interest, for it is in this genus that the majority of hallucinogenic species are found. *Psilocybe mexicana* and other related species are referred to collectively as the "sacred mushroom" (teonanácatl) used by the Mexican Indians for centuries in certain religious rites.

Although the existence and use of hallucinogenic mushrooms had been known for a long time, the subject received little attention by biologists until Professor Roger Heim, of the Natural History Museum of Paris, published three papers on the sacred mushrooms collected by Wasson and Wasson, and by Heim himself in their company, during their expeditions to Mexico. Wasson and Wasson (1957), in one of the most fascinating books published in our time, *Mushrooms, Russia, and History*, describe the ceremonies during which certain Mexican tribes use the sacred mushroom. These authors, having themselves partaken of the hallucinogenic fungi, have recorded the ecstatic effects which these mushrooms produce. Another treatise on this subject is the book by Heim and Wasson (1957/1958). These beautifully illustrated books have already become collectors' items. A short popular account of these experiences was published by *Life Magazine* (May 13, 1957).

Singer (1958) and Singer and Smith (1958) have summarized our knowledge concerning teonanácatl and have elucidated the taxonomy of the section of the genus *Psilocybe* in which hallucinogenic mushrooms belong. Some of these mushrooms have now been grown in culture, and the chemistry of the hallucinogenic substances has been worked out. One of these, psilocybin, has been synthesized and is being used experimentally in the study of schizophrenia (Hofmann *et al.*, 1958a, b; Hofmann, 1958; Hofmann *et al.*, 1959; Heim, 1961; Heim and Wasson, 1957/1958).

The purple-spored agarics include, among others, *Agaricus campestris*, the field mushroom, the superb *Agaricus rodmani* (see page 505 and Figure 179), and *Agaricus placomyces*. All three are considered edible, although some doubts have been expressed about the last (Smith, 1949).

Finally, in the black-spored agarics we find the many members of the genus *Coprinus* (the inky-cap mushrooms) whose gills deliquesce into a black, inky liquid which drips from the disintegrating cap. The shaggy-mane mushroom (*Coprinus comatus*) (Figure 186) is probably the best of these species. Other common species in this genus are *Coprinus micaceus* and *Coprinus atramentarius*.

One more word on the topic of mycophagy (Gr. *mykes* = mush-



Figure 186. *Coprinus comatus*. From Kodachrome transparency, courtesy E. S. Beneke.

room + *phagein* = to eat). Individuals differ in their reactions to mushrooms, and there are authentic cases of poisoning by mushrooms which many people can eat safely. It is, therefore, wise to eat only a relatively small quantity of a mushroom the first time, even though it has been correctly identified by a competent person and declared edible.

series GASTEROMYCETES

The Gasteromycetes include those Homobasidiomycetidae whose fruiting bodies either remain closed, or open only after the spores are mature. In most Gasteromycetes the hymenial layer is indistinct at the time of spore release, the basidia having already disintegrated. The Gasteromycetes as a general rule bear their spores symmetrically on the sterigmata. The spores are not discharged violently, as in other Basidiomycetes.

The fruiting bodies are characterized by a distinct outer wall (peridium) which may open naturally, in various ways, after the spores are mature and have fallen off the basidia, or may remain closed permanently, the spores being liberated only upon the disintegration of the peridium through the action of external agents. The fertile portion of the basidiocarp, enclosed by the peridium, we

call the *gleba* (pl. *glebae*; L. *gleba* = clod). The Gasteromycetes include the puffballs, the earthstars, the stinkhorns, and the bird's-nest fungi.

Classification. The number of gasteromycetous orders varies according to different authors. Smith (1951) divides the Gasteromycetes into ten orders. Martin (1961) lists the following orders as belonging to this series: Hymenogastrales, Lycoperdales, Sclerodermatales, Phallales, and Nidulariales. These may be distinguished in accordance with the characteristics in the simplified key on page 494.

order HYMENOGASTRALES

This order includes some forms which are intermediate in structure between the Hymenomycetes and the Gasteromycetes. The best-known genus is probably *Endoptychum*, *Endoptychum agaricoides* being commonly found in the United States. Its fructifications are stalked and more or less resemble mushrooms. A sterile columella is a prominent feature of many members of this order. In many species of Hymenogastrales, the gleba is fleshy or cartilaginous and is so formed as to resemble a lamellate structure; in other species the gleba is filled with jelly.

order LYCOPERDALES

The Lycoperdales include the common puffballs and some of the earthstars. At maturity, the powdery gleba, typically consisting of light-colored spores and well-developed capillitium, is surrounded by a peridium of two to four layers.

Smith (1951) subdivides the order, as he defines it, into six families. Martin (1961) recognizes but three: Arachniaceae, Lycoperdaceae, and Geastraceae. Members of the last two families are common and easy to recognize.

The Lycoperdaceae are the common puffballs. Some grow on tree stumps, on decaying logs, or on the ground in the woods. You can find other species, notably the giant puffballs, in city lawns, golf greens, and grassy, open fields. All species of puffballs are edible.¹ They are best when pure white inside. As the spores form, the center of the puffball begins to turn yellow and the flavor is spoiled by this time; even then, the puffball is not poisonous although it no longer tastes good.

The fruiting bodies of the Lycoperdaceae are enclosed by two

¹ But see some interesting remarks by A. H. Smith (1949) on this point.

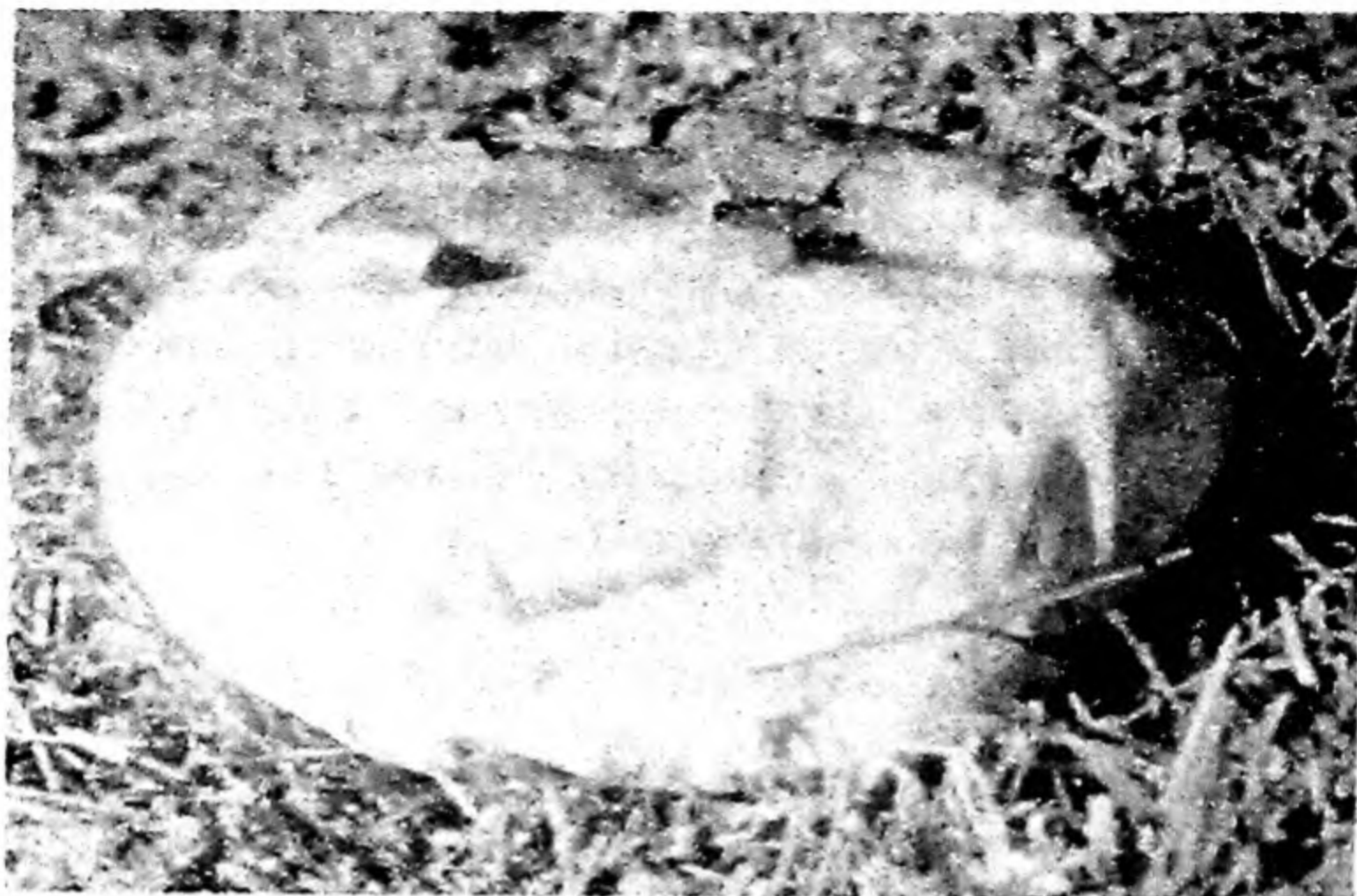


Figure 187. *Calvatia gigantea*. From Kodachrome transparency by the author.

peridial layers (inner and outer peridium). In the genus *Calvatia*, to which the giant puffball *Calvatia gigantea* (Figure 187) belongs, both peridial layers are quite thin and fragile. No special provision is made for the liberation of the spores, which are exposed when the peridial layers fragment. The fruiting bodies of the giant puffball sometimes exceed a long diameter of 3 or 4 feet. *Calvatia gigantea* has come into prominence recently with the discovery of calvacin, an antitumor agent present in aqueous extracts of the basidiocarps (Lucas *et al.*, 1959; Roland *et al.*, 1960).

The two layers which compose the peridium in *Lycoperdon* are quite distinct. When the outer layer weathers away, the inner, thin, membranous layer remains intact. It is provided with a small central opening (ostiole) from which the spores are puffed when an object strikes the membrane.

The development of *Lycoperdon oblongisporum* was studied by Ritchie (1948) at West Virginia. The sporophores, which do not exceed 2 cm. in diameter when mature, begin as tiny hyphal knots at the tips of very delicate rhizomorphs. At a very early stage numerous irregular, labyrinthine cavities begin to form in the center of the fruiting body, their formation spreading toward the periphery. As these cavities enlarge, great numbers of branches from the hyphae which form the walls of the cavities develop basidia at their tips. These hyphae are binucleate and so, of course, are the young basidia. The basidia are crowded together in a hymenium which completely

lines each cavity. The two nuclei in the basidium now fuse, and the zygote nucleus undergoes meiosis and forms four haploid nuclei. Long sterigmata now form on the basidium which produce the basidiospores at their tips. Each basidium normally forms four basidiospores. The nuclei then squeeze through the narrow sterigmata by becoming incredibly narrow and elongated. One nucleus enters each spore. If fewer than four spores form, the extra nuclei remain in the basidium. A thicker wall now develops around the basidiospore. At maturity, each basidiospore becomes binucleate by the division of its nucleus. When the basidiospores are fully formed, they fall off the basidium, each taking a portion of its sterigma with it. The spores completely fill the cavities. The basidia eventually disintegrate. Some of the hyphae which form the gleba become thick, heavy-walled, and pitted. These form the capillitium which, in the mature sporophore, is found intermingled with the spores. Other hyphae disintegrate.

Earthstars are puffballs in which the outer peridial layers split along radial fissures and when wet open out in the form of a star. The inner peridium remains closed except for one or more ostiolar openings through which the spores escape. *Geastrum* is the most

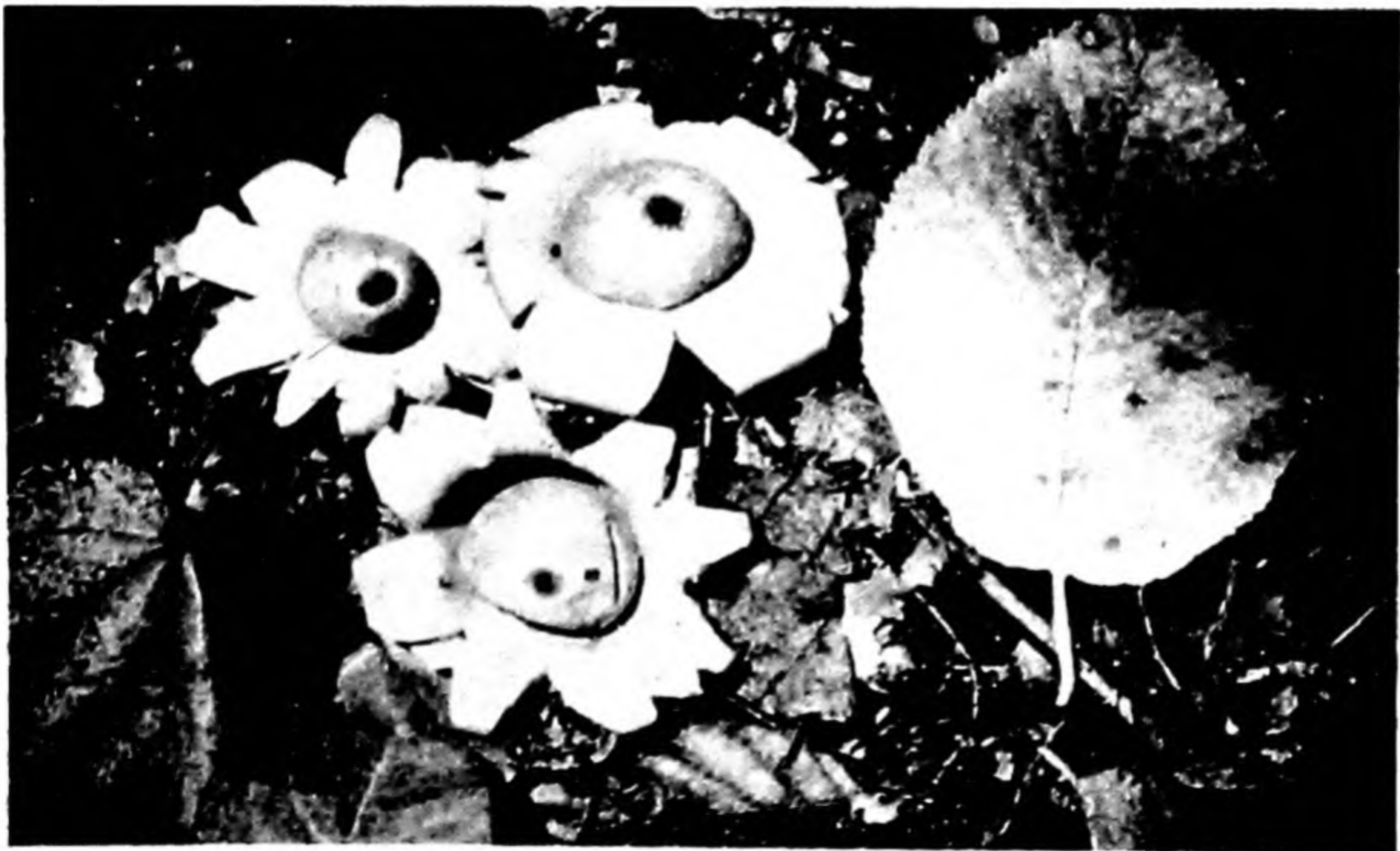


Figure 188. *Geastrum* sp. From Kodachrome transparency, courtesy J. A. Herrick.

common genus in the Geastraceae, the family to which most earthstars belong (Figure 188). The inner peridium opens by a single pore. In *Myriostoma* the membranous inner peridium rests on several short stalks. The spores escape through many small perforations.

order SCLERODERMATALES

You can recognize the more common of the Sclerodermatales by their thick, typically hard peridium and their usually dark gleba. The chief difference between this order and the Lycoperdales, however, is that the Lycoperdales have a distinct hymenium, at least in the early stages of development, whereas the Sclerodermatales lack a well-organized hymenium. Admittedly, such a character is a difficult one to determine.

Smith classifies the genera of the Sclerodermatales into seven families. Martin (1961) subdivides the order into four families: Sclerodermataceae, Astraeaceae, Tulostomataceae, and Calostomataceae.

Species of *Scleroderma*, the most common of the genera in the Sclerodermataceae, look like puffballs with a hard outer wall and a purplish-black gleba (Figure 189). *Astraeus* is the only genus in the Astraeaceae. These are earthstars with a very thick outer peridium consisting of several layers and dehiscing stellately. In *Astraeus hygrometricus*, the outer peridium is hygroscopic, opening and clos-



Figure 189. *Scleroderma* sp. From Kodachrome transparency, courtesy J. A. Herrick.

ing with alternate periods of wetting and drying. Of considerable interest are the stalked puffballs (family Tulostomataceae) which we classify in this order. The genus *Tulostoma* contains species with very small basidiocarps, their stalks not exceeding an inch or two in length supporting heads about $\frac{3}{8}$ inch in diameter. In the genus *Battarrea*, on the other hand, the stalk, which supports a puffball only about an inch or two in diameter, may exceed 12 inches in length.

order PHALLALES

The Phallales are the stinkhorns, so called because of the fetid odor that accompanies the exposure of the gleba, and the horn-like receptacle of most species which issues from the peridium raising the gleba to the surface.

The young fruiting body is whitish, egg-shaped, and, in some species, about the size of a hen's egg. The development of the stinkhorn, as we know it, takes place within the egg. The basidia and basidiospores are developed there, as well as all the other intricate structures that are evident when the eggs "hatch." The pressure caused by the enlargement of the internal organs finally breaks the peridium, and a long, spongy, pileate stalk emerges carrying the gleba on the surface of the receptacle. The "egg shell" (peridium) thus remains as a volva at the base of the stalk. In *Dictyophora duplicata*, a stinkhorn common to the eastern United States, the stalk has fully expanded 5 hours after the peridium splits, under favorable temperature conditions (Herrick, 1950) (Figures 190A, B, C, D). When the gleba-bearing receptacle of a stinkhorn has been exposed, the gleba undergoes autodigestion and the spores become enmeshed in a foul-smelling, gelatinous, greenish matrix which is said to be sweet, though how anyone had the courage to taste it is beyond comprehension. Flies are attracted by the odor—as only flies can be—and visit the sweet, sticky gleba, thus disseminating the spores, which cling to the mouth parts and bodies of the insects, and which pass through the alimentary tract.

The Phallales include some of the most beautiful of fungi. Unfortunately the odor which accompanies the expansion of the sporophore is so nauseating that all but the most ardent students of these forms prefer to admire them as preserved specimens well immersed in alcohol, and tightly sealed.

The structures of the stalk and receptacle vary considerably in different forms and constitute the basis on which genera are differentiated. In *Clathrus*, the receptacle resembles a lattice-work basket;

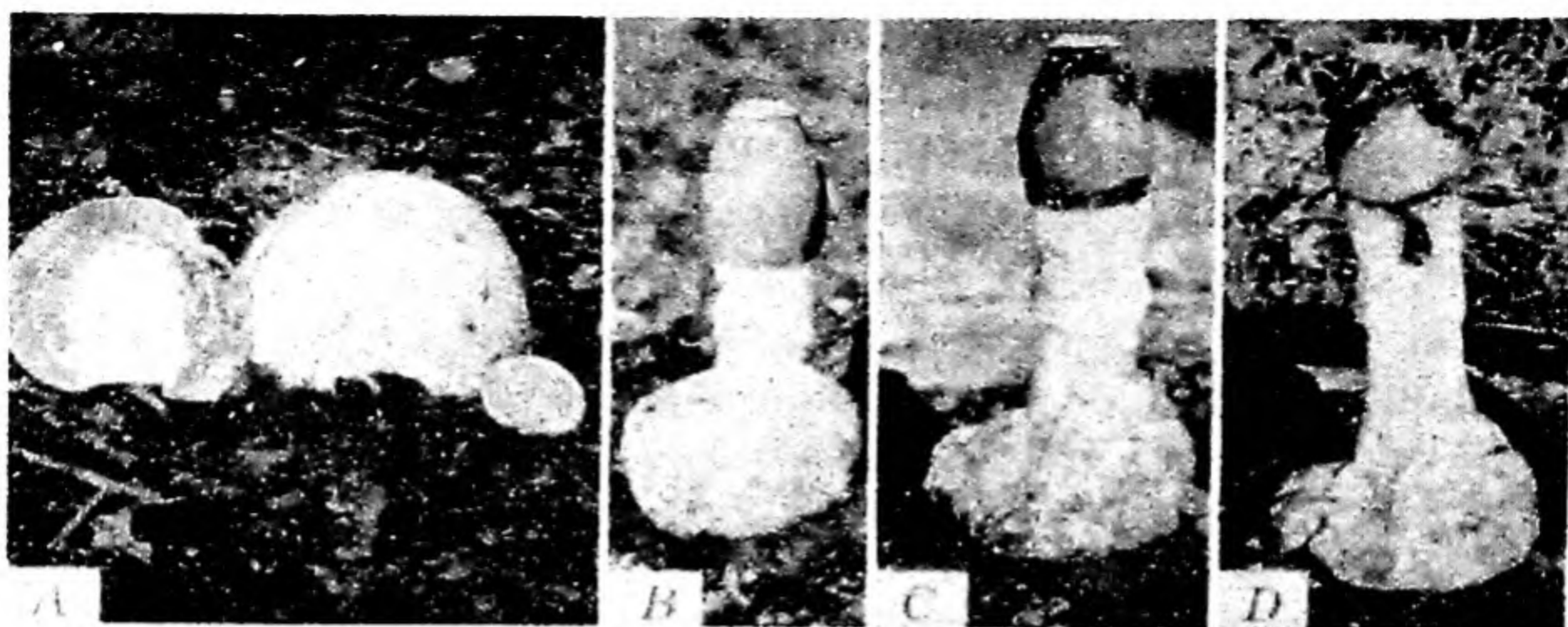


Figure 190. *Dictyophora duplicata*. A. "Eggs," the one on the left cut open to show internal structure, the one on the right with its peridium intact. B. Pileus 2 hours after the peridium first began to split. C. Same pileus 3 hours later, fully expanded. D. Same pileus 4 hours later. Note the deliquescent gleba and the fly feeding on the gelatinous substance. From Kodachrome transparency, courtesy J. A. Herrick.

in *Mutinus*, the stalk and receptacle are relatively slender, exhibiting brilliant colors, the stalk a rosy pink, the receptacle a deep red; *Phallus* (Figure 191) has a thick, spongy stalk which supports a ridged or pitted receptacle; *Dictyophora* (Figure 190) finally is like *Phallus* except for a beautifully perforated, lace-like, pure white

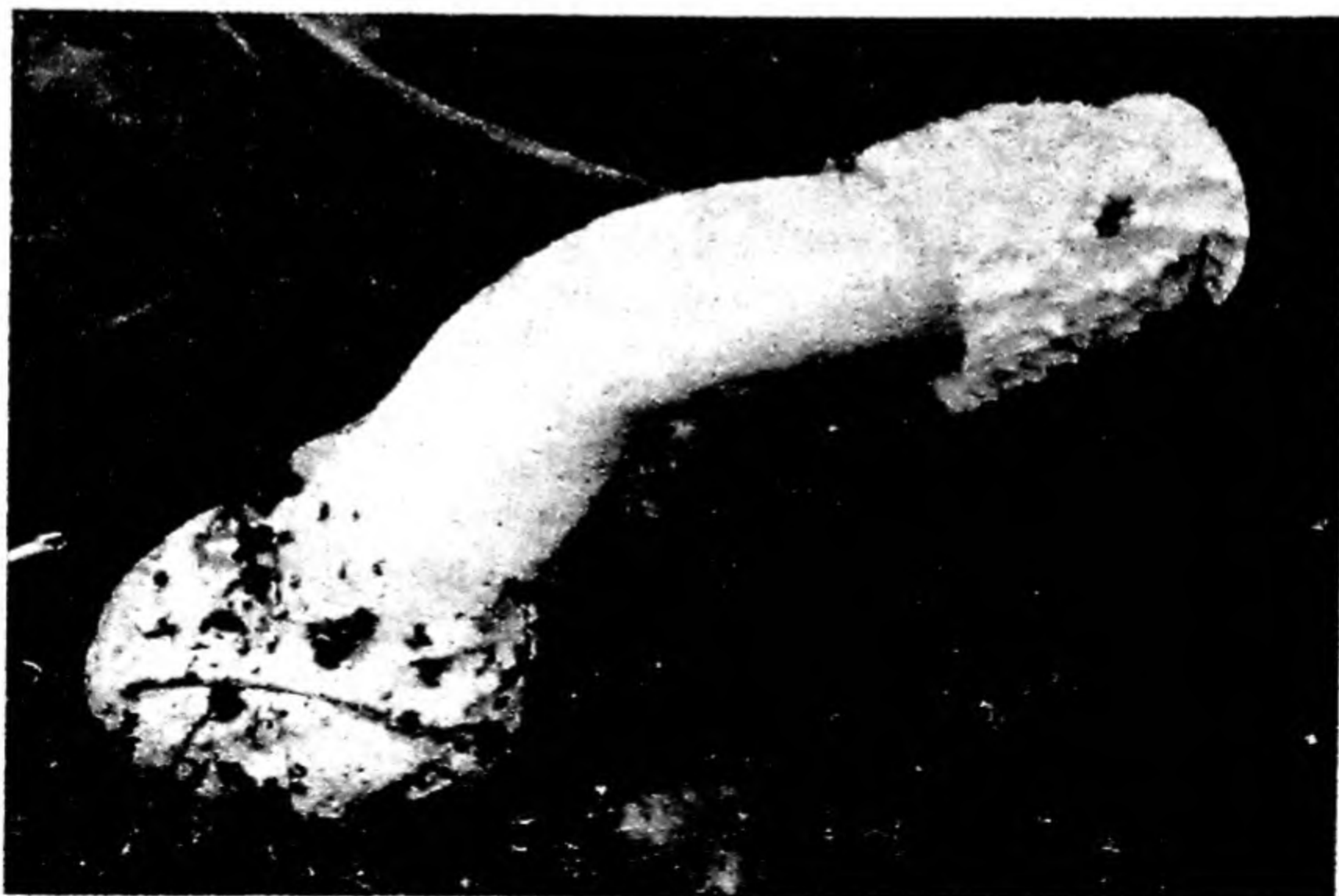


Figure 191. *Phallus impudicus*. From Kodachrome transparency, courtesy J. A. Herrick.

"skirt"—the *indusium* (pl. *indusia*; L. *indusium* = undergarment)—which hangs from the base of the receptacle.

order NIDULARIALES

The Nidulariales are the bird's-nest fungi. They are so called because the mature, hollow fruiting body contains a number of small, hard, lentil-shaped structures, neatly arranged within it, and thus resembles a miniature bird's nest containing eggs.

In this group of Gasteromycetes, each glebal chamber—formed in about the same way as described for *Lycoperdon*—becomes separated from the peridium and surrounded by several walls, the outer one of which is hard and waxy. Each glebal chamber thus becomes converted into a small lentil-shaped *peridiole* (Gr. *peridion* = small leather pouch + L. *-olum* = dimin. suffix), which contains the basidiospores. Several peridioles are formed within each cup-shaped fruiting body in the family Nidulariaceae. In the Sphaerobolaceae the entire gleba separates from the peridium and is violently discharged.

The family Nidulariaceae includes the common genera *Crucibulum* and *Cyathus* (Figure 192). *Nidula* and *Nidularia* are other often encountered genera. The fruiting bodies of *Crucibulum* are rather shallow; the peridioles are white. In *Cyathus* the fruiting body is deeper, shaped like an inverted bell; the peridioles appear dark gray or black (Figure 192). In these two genera each peridiole is attached to the inner surface of the cup by means of a slender mycelial connection, the *funiculus* (pl. *funiculi*; L. *funiculus* = a small cord). When wet, the funiculus expands greatly and may reach a length of 15–20 cm. Under such conditions the very base of the cord, the *hapteron* (pl. *haptera*; Gr. *hapto* = I touch), is quite sticky and adheres easily to solid objects after it is released from the cup.

B. O. Dodge (1941) discussed his observations and those of others on the dissemination of the peridioles. Dodge placed fruiting bodies on the ground under a Juneberry bush (*Amelanchier*). After about a month he found a number of the peridioles hanging by their funiculi from the leaves above the fruiting bodies. The funiculi were attached to the underside of the leaves and stretched from $\frac{1}{2}$ to 3 inches in length.

The mechanism of peridiole dissemination in *Cyathus* is very adequately explained by Brodie (1951b). According to Brodie, the cups of the bird's-nest fungi are so constructed as to act as splash-cups from which raindrops, during a heavy storm, striking with a terminal

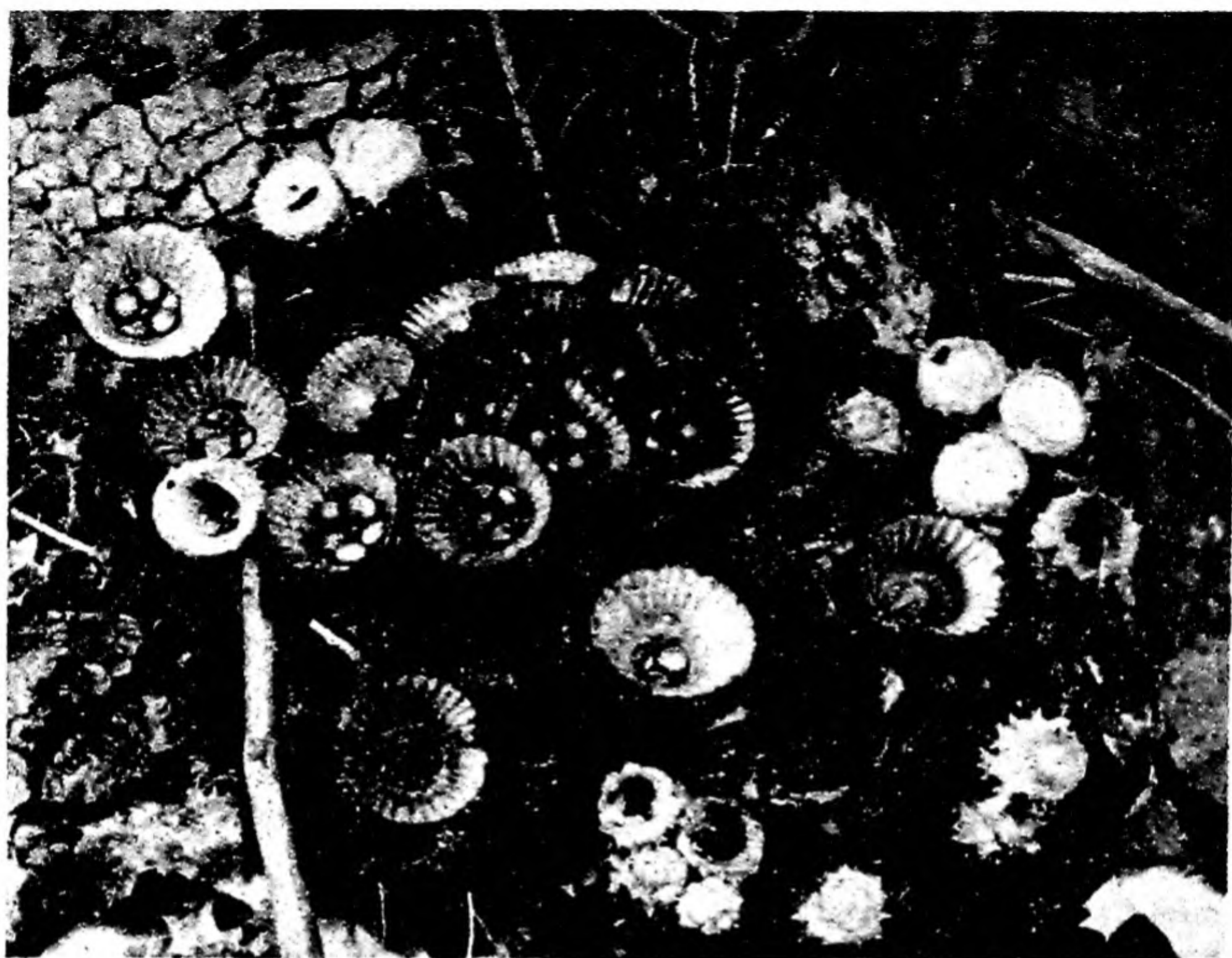


Figure 192. *Cyathus striatus*. Courtesy H. J. Brodie.

velocity in the neighborhood of 6 meters per second, eject the peridioles to a distance of 3–4 feet. The force of ejection causes that portion of the funiculus called the purse to burst and release the funicular cord and hapteron (Figures 193, 194C). The sticky hapteron, upon striking a solid object such as a nearby plant, adheres to it, and as the peridiole continues in flight the funicular cord expands to its full length (Figure 194D). Thus, the peridiole soon hangs down vertically or is wound around the object to which the hapteron is attached (Figure 194F).

Dissemination of the peridioles of the other genera of the Nidulariaceae undoubtedly takes place in a similar fashion. In *Nidula* and *Nidularia* which lack a funiculus, the peridioles are covered with an adhesive substance through which they adhere directly to the first solid surface they strike after being splashed out of the cup.

Dr. H. J. Brodie (1948a, 1948b, 1949, 1951a, 1951b) has grown a number of species of the Nidulariaceae in pure culture from single basidiospores. By mating various haploid mycelia he has obtained

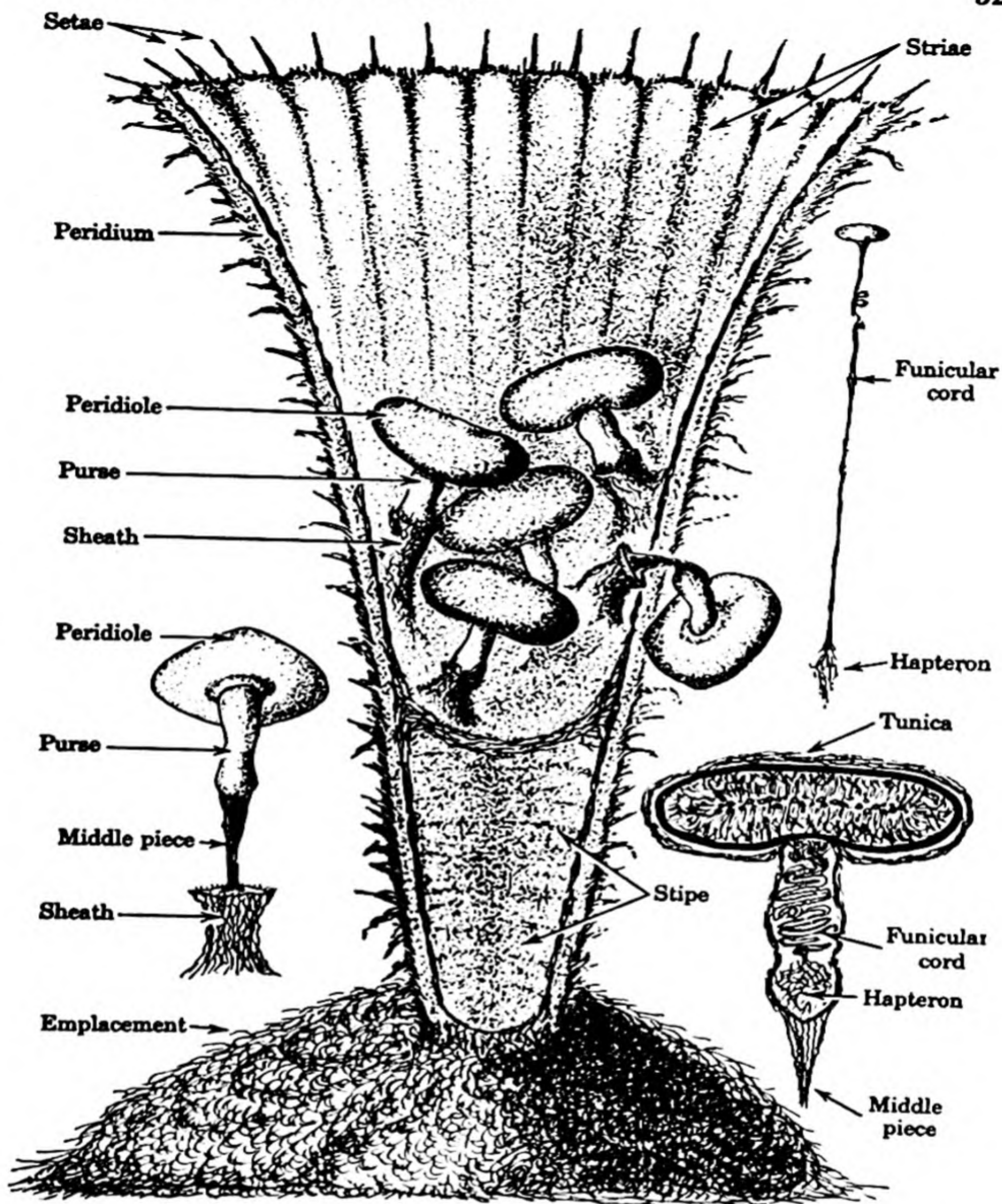


Figure 193. Section of fruit body of *Cyathus striatus* (semi-diagrammatic), showing names of various structures. Spores are borne inside the lenticular peridioles, each of which is attached to the inner wall of the fruit body by a funiculus consisting of sheath, middle piece, and purse. When a raindrop ejects a peridiole, the purse is torn open at its lower end, freeing the long funicular cord. Figure and legend courtesy Brodie, 1951, *Can. Jr. Bot.*, 29:224-234.

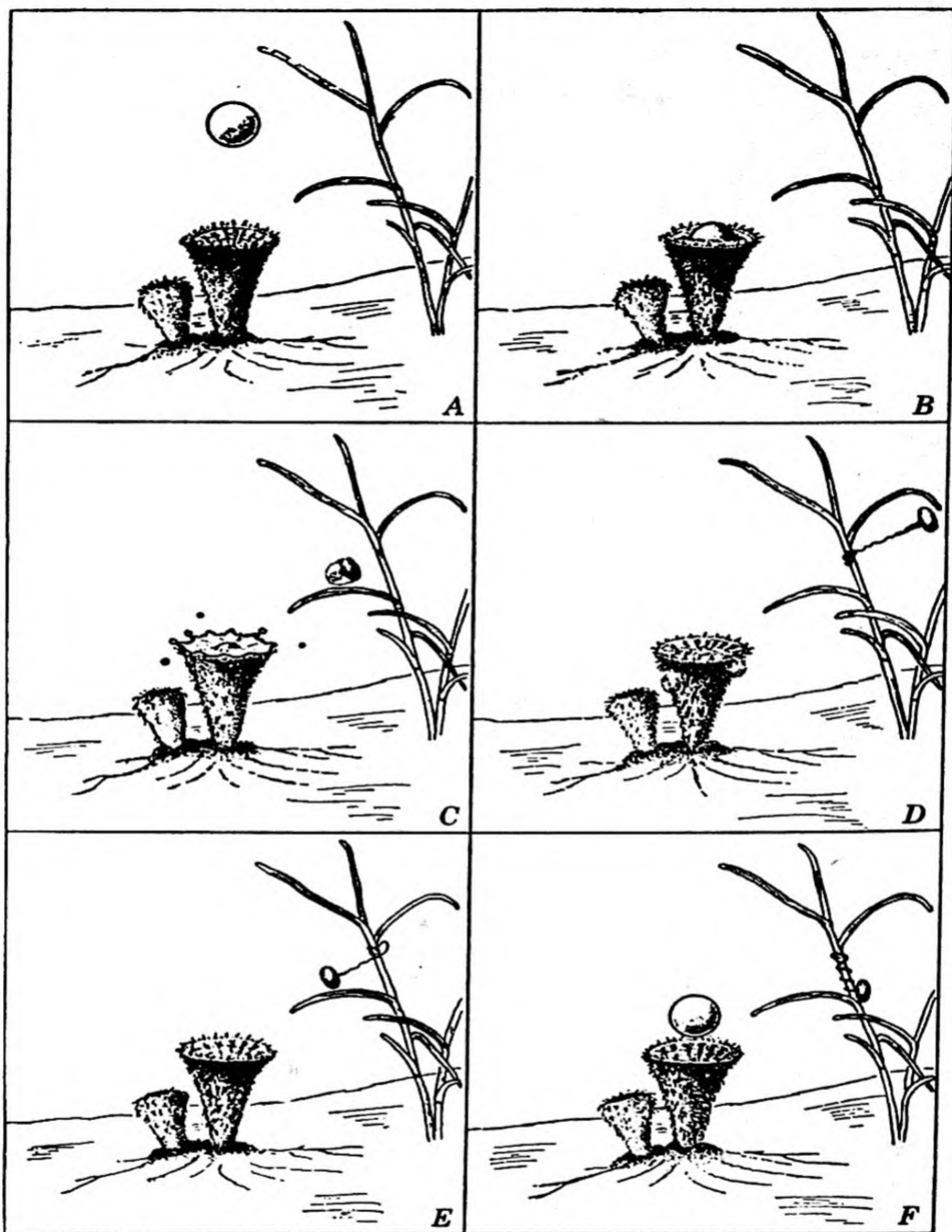


Figure 194. Diagram of the splashing of a peridiole from a fruit body of *Cyathus striatus*. A, B. Raindrop lands in cup. C. Splash action ejects peridiole which flies out with adhesive hapteron extended. D. Hapteron sticks to plant stem as peridiole is carried forward by its own momentum and funicular cord is extended by pull. E. Peridiole is jerked back when it reaches limit of extension of cord. F. Jerk causes peridiole to swing around point of attachment and cord is wrapped around plant stem as another raindrop lands in splash-cup. Figure and legend courtesy Brodie, 1951, *Can. Jr. Bot.*, 29:224-234.

fruiting bodies and has shown that all species studied thus far are tetrapolar.

You may remember that when we were discussing the Zygomycetes (Chapter 9) we mentioned *Pilobolus*, the fungal shotgun. In the family Sphaerobolaceae we have the genus *Sphaerobolus*, often called the fungus artillery. *Sphaerobolus* produces a more or less spherical fruiting body no larger than 2.5 mm. in diameter. This is so constructed that, after the peridium has split open at the top, exposing the upper half of the gleba, the tiny glebal ball is violently ejected. Walker and Andersen (1925) have explained the mechanism of the discharge. The peridium is composed of several layers, each different in structure from the others. After the peridium ruptures at the top, stored glycogen becomes transformed to reducing sugar. The increased osmotic pressure results in the stretching and sudden reversing of the peridial layer immediately below the gleba, thrusting the latter upward with an explosive force and propelling it through the air to a distance of more than 4 feet (Walker, 1927). The ejection of the gleba is said to be accompanied by an audible retort. This is a good note on which to close our discussion of the Basidiomycetes.

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PART V THE LICHENS

22 THE LICHENS

A lichen is an association of a fungus and an alga in which the two organisms are so intertwined as to form a single thallus. The fungus component of the lichen is called the **mycobiont** (Gr. *mykes* = fungus + *bios* = life), and the algal component is called the **phycobiont** (Gr. *phykos* = alga + *bios* = life). For a long time botanists thought the lichens were individual plants just like any other member of the plant kingdom, but they later discovered the dual nature of the lichen thallus. Nevertheless, because of the intimate association of the two components of the lichen thallus, and the rather unusual and definite shape that each lichen "species" assumes, botanists continue to classify the lichens into separate categories apart from the fungi and algae. Not only is this true, but also the relationship of the two organisms has been variously explained and variously named.

The lichen is said by some to represent an association between the fungus and the alga from which both partners benefit, and the association is held to be the perfect example of symbiosis which, through the ages, has modified the fungus and has caused the development of new structures peculiar to the symbiont. The fungus derives food from the algal cells and in return protects the alga from adverse conditions, particularly from drought.

Another group of botanists takes the opposite view, maintaining that the association of the alga and the fungus in a lichen is little different from a host-parasite relationship in which the parasitism of the fungus is weak, permitting most of the algal host cells to survive.

Botanists of a middle-of-the-road group, while agreeing in general that a symbiotic relationship exists between the fungus and the alga in the lichen thallus, state that the fungus holds the alga imprisoned in a state of slavery, helotism being the word used, thus granting that the fungus has the upper hand in the association between the two organisms.

Modern research is beginning to provide some answers to the lichen riddle. A large number of lichen fungi have now been grown in pure culture away from their algal hosts, and their physiology is being investigated. Henriksson (1958) showed that the mycobiont of the lichen *Collema tenax*, when grown in pure culture with the phycobiont (*Nostoc* sp.) of the same lichen and with other blue-green algae (*Cylindrospermium maius*, *Nostoc passerianum*, *Nostoc calcicola*), destroyed the algal cells in the vicinity of its hyphae. It appears also that, when the fungus is growing on an inorganic medium, the proximity of the cells of the phycobiont induces the fungal hyphae to produce rhizoid-like structures. Later, Ahmadjian and Henriksson (1959) grew the mycobiont of *Collema tenax* with *Trebouxia impressa*, the phycobiont of another lichen (*Physcia stellaris*), and reported that many of the algal cells died. Furthermore, a large percentage of the dead, empty cells were filled with fungal hyphae. In view of Henriksson's (1958) previous observations it appears probable that the dead algal cells had been killed by the fungus, especially since the control algal cultures (those without the fungus) appeared to be perfectly healthy.

As a result of these and many other observations, Ahmadjian (1960) raised the interesting question of what happens to the spores of the lichen mycobionts in nature after they have been released from the sporophores. As he points out, it is now known that specific mycobionts growing close to various algae contact the algal cells and accept them as hosts. Inasmuch as the cells of many species of algae thus contacted appear to be destroyed by direct or indirect fungal action, the specificity of the phycobiont of lichens appears to depend on the resistance of the phycobiont to fungal attack, the phycobionts which survive, forming lichens with the mycobionts associated with them.

Attempts to synthesize lichens by growing the two components together in culture have met with varied success (Bornet, 1873; Bonnier, 1889; Thomas, 1939; Ahmadjian, 1959, 1960/61). Recently published reports of experiments (Ahmadjian, 1962) with *Acarospora fuscata* indicate that this lichen may be synthesized by bringing together the phycobiont and mycobiont on media which will not support either separately. On media which favor the growth of either or both components separately no lichenization takes place.

It appears that the fungus parasitizes the algal cells and also lives saprobically on the algal cells which die, as a result of either parasitism or other causes. The alga survives under these conditions because of its association with the fungal pseudoparenchyma formed

in such cultures. Apparently the algal cells are protected from high light intensity, and it may be that the fungus also provides some nutrients (salts?) which the alga needs.

A very delicate balance thus exists in the relationship of the phycobiont and the mycobiont in a lichen thallus which, if disturbed in favor of either, may result in disassociation and, under certain conditions, destruction of the less-favored organism.

Of interest are the experiments reported by W. Lazo (1961), who grew plasmodia of *Myxomycetes* with algae in an attempt to synthesize a "myxolichen." The plasmodium incorporated the algal cells and became vivid green in color when the cultures were grown in the light on a medium favorable for plasmodial growth. Portions of the green plasmodia transferred to a favorable medium continued to grow and remained green, indicating that the algae in the association multiplied. However, on a medium favorable to algal but not to plasmodial growth, the plasmodium/alga combination did not thrive (Lazo, unpublished results), showing that the plasmodium was unable to utilize either the algal cells or their products as sources of energy.¹

The fungi which parasitize microscopic algae forming lichens are either *Pyrenomycetes* (*Pyrenolichens*), *Discomycetes* (*Discolichens*), or members of the *Thelephoraceae* in the *Agaricales* (*Basidiolichens*).

The so-called lichen fungi, being no different from other *Ascomycetes* or *Basidiomycetes*, should be classified in the orders of these two classes in which their structural features place them. To classify them as we do at present on the basis of both host and parasite structures is admittedly convenient, but certainly does not indicate their relationships to other fungi. To incorporate them in the existing system of classification would necessitate a change of names, inasmuch as the present binomials are not given to the fungus but to the host-parasite combination. Ciferri and Tomaselli (1953) have placed all the lichen fungi in new genera, taking the name of each lichen "genus" and adding *-myces* to it. Thus the mycobionts of *Collema* are assigned to the new genus *Collemomyces*, etc. This does not accomplish what has been suggested above unless we assume, as they do, that none of the lichen mycobionts can be fitted in any of the recognized fungal genera.

The lichenological literature, most of it taxonomic and phytogeographic, is enormous. A small and very readable treatment of the

¹ But see Zabka and Lazo (1962).

lichen problem is Mason Hale's *Lichen Handbook*, published by the Smithsonian Institution. A good bibliography is included.

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PART VI GLOSSARY

GLOSSARY OF MYCOLOGICAL TERMS USED IN THE TEXT

Key to symbols: Gr. = Greek; Icel. = Icelandic; L. = Latin; ME. = Middle English; NL. = New Latin.

Acervulus (pl. *acervuli*; L. *acervus* = heap, dimin. form): a mat of hyphae giving rise to short conidiophores closely packed together forming a bed-like mass. Characteristic of the Melanconiales. (Figures 80B, 141.)

Achlorophyllous (Gr. *a* = not + *chloros* = green + *phyllon* = leaf): lacking chlorophyll.

Aeciospore (Gr. *aikia* = injury + *sporos* = seed, spore): a binucleate spore produced in an aecium (Figure 161).

Aecium (pl. *aecia*; Gr. *aikia* = injury): a structure consisting of binucleate hyphal cells, with or without a peridium, which produce spore chains consisting of aeciospores alternating with disjuncter cells, by the successive, conjugate division of the nuclei (Figure 161).

Aethalium (pl. *aethalia*; Gr. *aethalos* = soot): a rather large, sometimes massive, generally cushion-shaped fructification of some Myxomycetes (Figure 35).

Akaryote (Gr. *a* = not + *karyon* = nut, nucleus): a phase in the life cycle of the Plasmodiophorales during which the nucleoplasm loses its affinity for stains (Figures 64N, 65N).

Anisogamous planogametes (Gr. *a* = not + *isos* = equal + *gamos* = marriage; *planetes* = wanderer + *gametes* = husband): motile gametes which are morphologically similar but which differ in size (Figure 14B).

Anisogamy (Gr. *a* = not + *isos* = equal + *gamos* = marriage, union): union of planogametes which are morphologically similar but which differ in size (Figure 14B).

Annulus (pl. *annuli*; L. *annulus* = ring): the ring found on the stem of certain species of mushrooms. Remnant of the inner veil. (Figure 180.)

Antheridium (pl. *antheridia*; Gr. *antheros* = flowery + *-idion*, a dimin. suffix): a male gametangium (Figure 15).

Antherozoid (Gr. *antheros* = flowery + *zoidion* = little animal): the motile male gamete of the Monoblepharidales (Figure 46E).

Antibiotic (Gr. *anti* = against + *bios* = life): a substance produced by a living organism, which injures or kills another living organism.

Aphanoplasmodium (pl. *aphanoplasmodia*; Gr. *aphanes* = invisible + *plasmodium*): a plasmodium consisting, in its early stages, of a network of very fine transparent strands which are not conspicuously differentiated into ecto-

and endoplasm, and in which the protoplasm is not coarsely granular.

Characteristic of *Stemonitis* and possibly other related genera. (Figure 31.)

Aplanetic (Gr. *a* = not + *planetes* = wanderer): non-motile.

Aplanospore (Gr. *a* = not + *planetes* = wanderer + *sporos* = seed, spore): a non-motile spore (Figures 70C, C').

Apothecium (pl. apothecia; Gr. *apothēke* = storehouse): an open ascocarp (Figure 85D).

Appressorium (pl. appressoria; L. *apprimere* = to press against): a flattened, hyphal, pressing organ, from which a minute infection peg usually grows and enters the epidermal cell of the host.

Archicarp (Gr. *arche* = beginning + *karpos* = fruit): the initial stage of a fruiting body.

Arthrospore (Gr. *arthron* = joint + *sporos* = seed, spore): a spore resulting from the fragmentation of a hypha. Also called oidium. (Figures 9A, 143B, C.)

Ascigerous (Gr. *askos* = sac): the ascus stage of an ascomycete.

Ascocarp (Gr. *askos* = sac + *karpos* = fruit): a fruiting body containing asci (Figures 85B, C).

Ascogenous hypha (Gr. *askos* = sac + *gennao* = I give birth + *hyphe* = web): a specialized hypha which gives rise to one or more asci (Figures 82D, J).

Ascogonium (pl. ascogonia; Gr. *askos* = sac + *gennao* = I give birth): the female gametangium of the Ascomycetes (Figure 82A).

Ascospore (Gr. *askos* = sac + *sporos* = seed, spore): a spore, which results from meiosis, borne in an ascus (Figures 82L, 84).

Ascostroma (pl. ascostromata; Gr. *askos* = sac + *stroma* = mattress, cushion): a stromatic ascocarp bearing asci directly in locules within the stroma (Figures 130G, 132M).

Ascus (pl. asci; Gr. *askos* = sac): a sac-like structure generally containing a definite number of ascospores (typically eight) which are usually formed as a result of karyogamy and meiosis. Characteristic of the class Ascomycetes. (Figure 83.)

Ascus mother cell: The binucleate crook cell in the Ascomycetes in which karyogamy occurs and which develops into the ascus (Figure 82G).

Aseptate (L. *ab* = away + *septum* = hedge): lacking cross-walls (Figure 2A).

Asexual (L. *ab* = away + *sexus* = sex): reproduction not involving union of two nuclei (Figures 9, 12).

Aspergillois (*Aspergillus* = a genus of Deuteromycetes): one of a group of diseases of animals and human beings caused by various species of *Aspergillus*.

Asporogenous (Gr. *a* = not + *sporos* = seed, spore + *gennao* = I give birth): non-spore-forming.

Autoecism (Gr. *autos* = self, i.e., the same + *oikos* = home): the ability of a parasitic fungus to complete its entire life cycle on a single host species. Used particularly for certain rusts.

Axenic (Gr. *a* = not + *xenos* = stranger): without another organism being present.

Azygospore (Gr. *a* = not + *zygos* = yoke + *sporos* = seed, spore): a zygosporangium which develops parthenogenetically.

Basidiocarp (Gr. *basidion* = small base, basidium + *karpos* = fruit): a fruiting body which bears basidia (Figures 152, 154, 180).

Basidiospore (Gr. *basidion* = small base + *sporos* = seed, spore): a spore borne on the outside of a basidium, resulting from karyogamy and meiosis (Figure 150).

- Basidium** (pl. basidia; Gr. *basidion* = a small base): a structure bearing on its surface a definite number of basidiospores (typically four) which are usually formed as a result of karyogamy and meiosis (Figure 150).
- Binomial** (L. *bi* = two + *nomen* = name): the scientific name of an organism. It is composed of two names, the first designating the genus, and the second the species.
- Bipolar heterothallism**: see **Bipolarity**.
- Bipolarity** (L. *bi* = two + Gr. *polos* = pole): a condition of sexual compatibility in certain Basidiomycetes in which two basidiospores of each basidium are of one strain, and two are of another.
- Bitunicate** (L. *bis* = twice, two + *tunica* = coat, mantle): an ascus in which the inner wall is elastic and expands greatly beyond the outer wall at the time of spore liberation (Figures 87E, 131C, E).
- Blastospore** (Gr. *blastos* = bud, shoot + *sporos* = seed, spore): an asexual spore formed by budding (Figures 143A, B).
- Blepharoplast** (Gr. *blepharis* = eyelash + *plastid*): a cytoplasmic granule from which a flagellum originates.
- Budding** (ME. *budde* = bud): the production of a small outgrowth (bud) from a parent cell. A method of asexual reproduction. (Figure 11B.)
- Capillitium** (pl. capillitia; L. *capillus* = hair): sterile, thread-like structures present among the spores in the fruiting bodies of many Myxomycetes and Gasteromycetes (Figure 38).
- Centrum** (pl. centra; Gr. *keptron* = center): the totality of structures enclosed by the ascocarp wall.
- Chlamydospore** (Gr. *chlamys* = mantle + *sporos* = seed, spore): a hyphal cell, enveloped by a thick cell wall, which eventually becomes separated from the parent hypha and behaves as a resting spore (Figure 9B).
- Cirrus** (pl. cirrhi; L. *cirrus* = curl): a ribbon-like cylinder of spores held together by mucus as it issues from an ostiole (Figure 138F).
- Clamp connection**: a bridge-like hyphal connection characteristic of the secondary mycelium of many Basidiomycetes (Figures on page 429).
- Cleistothecium** (pl. cleistothecia; Gr. *kleistos* = closed + *theke* = case): a completely closed ascocarp (Figure 85B).
- Coenocytic** (Gr. *koinos* = common + *kytos* = a hollow vessel): non-septate; referring to the fact that the nuclei are embedded in the cytoplasm without being separated by cross-walls, i.e., the nuclei lie in a common matrix (Figure 2A).
- Colony** (L. *colonia* = a settlement): a group of individuals of the same species living in close association. In fungi, the term usually refers to many hyphae growing out of a single point and forming a round or globose thallus. (Figure 10.)
- Columella** (pl. columellae; L. *columen* = column): a sterile structure within a sporangium or other fructification; often an extension of the stalk (Figures 37, 66A).
- Compound oösphere** (Gr. *oön* = egg + *sphaira* = sphere): an oösphere with many functional gamete nuclei.
- Conidiophore** (Gr. *konis* = dust + *phoreus* = bearer): a specialized hypha bearing conidia (Figure 79).
- Conidium** (pl. conidia; Gr. *konis* = dust + *-idion*, dimin. suffix): a spore formed asexually, usually at the tip or side of a hypha (Figures 79, 141, 142).

- Conjugate nuclear division** (L. *con* = with + *jugum* = yoke): the simultaneous division of the two nuclei in a dikaryon, giving rise to four daughter nuclei. These generally become separated by a septum into two cells, the sister nuclei migrating into different daughter cells.
- Context** (L. *contexere* = to weave together): the fibrous tissue which makes up the body of the pileus in the Basidiomycetes.
- Coprophilous** (Gr. *kopros* = dung + *philein* = to love): growing on dung.
- Cortina** (pl. *cortinae*; L. *cortina* = curtain): a curtain-like, cobwebby veil hanging from the margin of the cap of certain mushrooms.
- Cruciform** (L. *crux* = cross): intranuclear division in which the chromosomes are arranged in a ring around a dumbbell-shaped nucleolus as they divide. Found in the Plasmodiophoromycetes and some protozoa.
- Cystidium** (pl. *cystidia*; Gr. *kystis* = bladder + *-idion*, dimin. suffix): a large sterile structure in the hymenium of a basidiomycete (Figure 148).
- Damping-off**: a disease of seedlings which causes them to rot at the soil level and to fall over.
- Dermatomycosis** (Gr. *derma* = skin + *mykes* = mushroom): a fungous infection of animal or human skin.
- Dermatophyte** (Gr. *derma* = skin + *phyton* = plant): any one of several fungi which cause skin diseases.
- Dictyospore** (Gr. *dictyon* = net + *sporos* = seed, spore): a spore with both vertical and horizontal septa (Figures 12 upper left, 84R, 131G, 144H).
- Dikaryon** (NL. *di* = two + Gr. *karyon* = nut, nucleus): a pair of closely associated nuclei, each usually derived from a different parent cell.
- Dikaryotic** (NL. *di* = two + Gr. *karyon* = nut, nucleus): pertaining to a cell which contains a dikaryon (Figure 82E).
- Dimorphic** (Gr. *dis* = twice + *morphe* = form): producing two types of zoöspores.
- Dioecious** (NL. *di* = two + Gr. *oikos* = home): refers to species in which the sexes are segregated in different individuals (Figure 129). The use of this term is often restricted to higher plants.
- Diplanetic** (Gr. *dis* = twice + *planetes* = wanderer): refers to a species which produces two types of zoöspores and in which two swarming periods occur (Figures 54C-F).
- Diploid** (Gr. *diploos* = double): containing the double ($2n$) number of chromosomes.
- Dolipore septum** (L. *dolium* = large jar + *pore*): a septum which flares out in the middle portion of a hypha, forming a barrel-shaped structure with open ends (Figure 147).
- Ectal excipulum** (Gr. *ektós* = outside + L. *excipulum* = receptacle): the outer layer of the apothecium (Figure 119).
- Egg** (Icel. *egg* = egg): female gamete (Figure 52A).
- Endobiotic** (Gr. *endos* = inside + *bios* = life): an organism which lives within its substratum, usually the cells of its host.
- Endoconidium** (pl. *endoconidia*; Gr. *endos* = inside + *conidium*): an asexual spore formed inside a hypha (endogenously) and extruded (Figures 106, 107).
- Epibasidium** (pl. *epibasidia*; Gr. *epi* = upon + *basidion* = small base): the upper portion of the basidial apparatus of the Heterobasidiomycetidae (Figures 155I-K).

- Epibiotic** (Gr. *epi* = on + *bios* = life): an organism whose reproductive organs are on the surface of the substratum, but part or all of whose soma is within the substratum.
- Epigean** (Gr. *epi* = upon + *ge* = earth): above the ground.
- Epiphytotic** (Gr. *epi* = upon + *phyton* = plant): a widespread occurrence of a plant disease.
- Epithecium** (pl. *epithecia*; Gr. *epi* = upon + *theke* = a case): a layer of tissue on the surface of the hymenium of an apothecium, formed by the union of the tips of the paraphyses over the asci.
- Epixylous** (Gr. *epi* = upon + *xylon* = wood): occurring on wood.
- Epizootic** (Gr. *epi* = upon + *zoön* = animal): a widespread occurrence of an animal disease.
- Eucarpic** (Gr. *eu* = good + *karpos* = fruit): forming reproductive structures on certain portions of the thallus, the thallus itself continuing to perform its somatic functions.
- Excipulum** (pl. *excipula*; NL. *excipulum* = receptacle): the outer layer of the hypothecium (Figure 119).
- Exoconidium** (pl. *exoconidia*; Gr. *exo* = outside + *conidium*): any asexual spore formed on the surface of a hypha (exogenously) (Figure 79).
- Facultative parasite** (L. *facultas* = ability; Gr. *parasitos* = table mate): an organism capable of infecting another living organism or of growing on dead organic matter, according to circumstances.
- Facultative saprobe** (L. *facultas* = ability; Gr. *sapros* = rotten + *bios* = life): an organism capable of growing on dead organic matter, or of infecting another living organism, according to circumstances.
- Fairy ring**: a ring of mushrooms on the ground representing the periphery of mycelial growth of a basidiomycete.
- Fertilization tube** (L. *fertilis* = fertile): a tube originating from the male gametangium and penetrating into the female, through which the male gametes (nuclei) are transferred (Figure 15).
- Fission** (L. *fissio* = splitting): the splitting of a cell into two cells (Figure 11A).
- Flagellum** (pl. *flagella*; L. *flagellum* = whip): a hair-, whip-, or tinsel-like structure which serves to propel a motile cell (Figures 13, 28, 63).
- Fragmentation** (L. *frangere* = to break): the segmentation of the thallus into a number of fragments each of which is capable of growing into a new individual. A method of asexual reproduction. (Figure 10.)
- Fructification** (L. *fructus* = fruit): any fungal structure which contains or bears spores.
- Fruiting body**: see **Fructification**.
- Fungus** (pl. *fungi*; L. *fungus* = mushroom): one of the achlorophyllous thallophytes whose somatic structures are usually filamentous and branched. Fungi have cell walls and demonstrable nuclei. They reproduce typically by both sexual and asexual means.
- Funiculus** (pl. *funiculi*; L. *funiculus* = a small cord): a thin cord by means of which the peridioles of some Nidulariales are attached to the basidiocarp which bears them. (Figure 193.)
- Gametangial contact** (Gr. *gametes* = husband + *angelon* = vessel): a method of sexual reproduction in which two gametangia come in contact but do not fuse. The male nucleus migrates through a pore or fertilization tube into the female gametangium. (Figure 15.)

- Gametangial copulation** (Gr. *gametes* = husband + *angeion* = vessel): a method of sexual reproduction in which two gametangia or their protoplasts fuse and give rise to a zygote which develops into a resting spore (Figures 16, 43E, F; 89C, 90C).
- Gametangium** (pl. gametangia; Gr. *gametes* = husband + *angeion* = vessel): a structure which contains gametes.
- Gamete** (Gr. *gametes* = husband, sex cell): a differentiated sex cell or a sex nucleus which fuses with another in sexual reproduction (Figures 14, 15).
- Gametothallus** (pl. gametothalli; Gr. *gametes* = husband + *thallos* = shoot): a thallus which produces gametes, as opposed to a sporothallus (Figures 45A, B).
- Gemma** (pl. gemmae; L. *gemma* = bud): a thick-walled cell similar to a chlamydospore (Figure 51).
- Genus** (pl. genera; L. *genus* = race): a taxonomic category which includes a number of species. The genus name (generic name) is the first name in a binomial.
- Gleba** (pl. glebae; L. *gleba* = clod): the inner, fertile portion of the fruiting body of the Gasteromycetes.
- Haploid** (Gr. *haplous* = simplex): containing the reduced (n) number of chromosomes.
- Hapteron** (pl. haptera; Gr. *hapto* = I touch): a mass of highly adhesive hyphae which form an attachment organ at the base of the funicular cord of the Nidulariaceae (Figure 193).
- Haustorium** (pl. haustoria; L. *haustor* = drinker): an absorbing organ originating on a hypha of a parasite and penetrating into a cell of the host. Most often associated with obligate parasites, but also produced by some facultative parasites. (Figures 5, 56.)
- Helicospore** (Gr. *helix* = helix + *sporos* = seed, spore): a coiled or helical spore (Figure 12, upper right).
- Helotism** (Gr. *heilotia* = serfdom): the name applied to the relationship of the alga to the fungus in a lichen, by those who do not concede that it is strict parasitism.
- Hermaphroditic** (Gr. *Hermes* = the messenger of the gods, symbol of the male sex + *Aphrodite* = the goddess of love, symbol of the female sex): refers to species in which both male and female sex organs are produced by each individual (Figure 45B).
- Heteroecism** (Gr. *heteros* = other, different + *oikos* = home, i.e., host): the necessity of two host species for the completion of the life cycle of certain parasitic fungi.
- Heterogametangia** (sing. heterogametangium; Gr. *heteron* = other, different + *gametes* = husband + *angeion* = vessel): male and female gametangia which are distinguishable morphologically (Figure 15).
- Heterogametes** (Gr. *heteros* = other, different + *gametes* = husband): male and female gametes which are distinguishable morphologically (Figure 14C).
- Heterokaryosis** (Gr. *heteros* = other + *karyon* = nut, nucleus): a condition in which genetically different nuclei are associated in the same protoplast.
- Heterokaryotic** (Gr. *heteros* = other + *karyon* = nut, nucleus): an individual exhibiting heterokaryosis.
- Heterokont** (Gr. *heteros* = other + *kontos* = staff): a biflagellate structure with two flagella, unequal in size (Figure 63).

- Heterothallic** (Gr. *heteros* = other, different + *thallos* = shoot, thallus): According to one version: refers to a species consisting of self-sterile (self-incompatible) individuals, requiring therefore the union of two compatible thalli for sexual reproduction, regardless of the possible presence of both male and female organs on the same individual. According to another version: refers to a species in which the sexes are segregated in separate thalli, two different thalli being required for sexual reproduction.
- Heterothallism** (Gr. *heteros* = other, different + *thallos* = shoot, thallus): the condition exemplified by heterothallic species.
- Holobasidium** (pl. holobasidia; Gr. *holon* = entire + *basidion* = a small base): a simple, club-shaped structure in which karyogamy and meiosis occur, and which bears basidiospores on its surface (Figure 149).
- Holocarpic** (Gr. *holos* = entirely + *karpos* = fruit): refers to an organism whose thallus is entirely converted into one or more reproductive structures.
- Holozoic** (Gr. *holos* = entirely + *zoikos* = of animals): ingesting food in the form of solid particles.
- Homokaryotic** (Gr. *homo* = the same + *karyon* = nut, nucleus): an individual whose nuclei are genetically alike.
- Homothallic** (Gr. *homo* = same + *thallos* = shoot, thallus): refers to fungi in which sexual reproduction takes place in a single thallus which is, therefore, essentially self-compatible.
- Homothallism** (Gr. *homo* = same + *thallos* = shoot, thallus): the condition exemplified by homothallic species.
- Host** (L. *hospes* = one who receives a stranger as his guest): a living organism harboring a parasite.
- Hyaline** (Gr. *hyalinos* = made of glass, i.e., colorless): colorless, transparent.
- Hymenium** (pl. hymenia; Gr. *hymen* = membrane): a fertile layer consisting of asci or basidia (Figures 85C, D; 148).
- Hyperplasia** (Gr. *hyper* = over + *plasis* = molding, formation): excessive multiplication of cells; abnormal rate of cell division.
- Hypertrophy** (Gr. *hyper* = over + *trophe* = food): excessive enlargement of cells.
- Hypha** (pl. hyphae; Gr. *hyphe* = web): the unit of structure of the fungi; a tubular filament (Figure 2).
- Hyphal body** (Gr. *hyphe* = web); a fragment of the mycelium of the Entomophthorales (Figure 73A).
- Hyphopodium** (pl. hyphopodia; Gr. *hyphe* = web + *pous* = foot): a small appendage on a hypha. Characteristic of the Meliolales.
- Hypobasidium** (pl. hypobasidia; Gr. *hypo* = under + *basidion* = small base): the basal portion of the basidial apparatus of the Heterobasidiomycetidae (Figure 155I).
- Hypogean** (Gr. *hypo* = under + *ge* = earth): growing below the ground.
- Hypothallus** (pl. hypothalli; Gr. *hypo* = under + *thallos* = shoot, thallus): a thin, often transparent deposit at the base of the fructifications of some Myxomycetes.
- Hypothecium** (pl. hypothecia; Gr. *hypo* = under + *theke* = case): a thin layer of interwoven hyphae immediately below the hymenium of an apothecium (Figure 119).
- Indusium** (pl. indusia; L. *industum* = undergarment): a skirt-like structure hanging from the receptacle of the expanded fruiting body of *Dictyophora* (one of the stinkhorns) (Figure 190).

- Inner veil:** the hyphal membrane which covers the gills of a young mushroom.
- Isogametangia** (sing. *isogametangium*; Gr. *ison* = equal + *gametes* = husband + *angeion* = container): gametangia, presumably of opposite sex, which are indistinguishable morphologically (Figure 16A).
- Isogametes** (Gr. *isos* = equal + *gametes* = husband): gametes, presumably of opposite sex, which are indistinguishable morphologically (Figure 14A).
- Isoplanogametes** (Gr. *isos* = equal + *planetes* = wanderer + *gametes* = husband): motile gametes, presumably of opposite sex, which are indistinguishable morphologically (Figures 14A, 41E, 42J).
- Karyallagy** (Gr. *karyon* = nut, nucleus + *allage* = change): fusion of sexually undifferentiated cells.
- Karyogamy** (Gr. *karyon* = nut, nucleus + *gamos* = marriage, union): the fusion of two nuclei (Figure 45G).
- Lamella** (pl. *lamellae*; L. *lamina* = plate, dimin. form): a plate-like structure (gill) on which some Basidiomycetes produce their basidia (Figure 180).
- Lichen** (Gr. *lichen* = lichen): a combination of an alga and a fungus in which the two components are so interwoven as to form what appears to be a single individual.
- Locule** (L. *loculus* = a little place): a cavity within a stroma.
- Macroconidium** (pl. *macroconidia*; Gr. *makron* = long + *konis* = dust + *-idion*, dimin. suffix): a conidium, as distinguished from a microconidium (Figures 113C, D).
- Macrocytic** (Gr. *makros* = long + *kyklos* = circle, cycle): long-cycled. Applied to those species of rusts which produce one or more types of binucleate spores in addition to teleutospores.
- Macrocyst** (Gr. *makros* = long, large + *kystis* = bladder): protoplasmic, walled, usually multinucleate portions of a myxomycete sclerotium. Also walled cell masses produced by the Acrasiales.
- Mazaedium** (pl. *mazaedia*; Gr. *maza* = dough + *eidōs* = like): a fruiting body in which the spores, freed from the asci, form a powdery mass.
- Medium** (pl. *media*; L. *medium* = intermediate): substratum of a balanced chemical composition employed in the laboratory for growing microorganisms. Media may be used in the liquid state or solidified with agar, gelatin, or other solidifying agents.
- Medullary excipulum** (L. *medulla* = marrow + *excipulum* = receptacle): the inner portion of the apothecium (Figure 119).
- Meiosis** (Gr. *meiosis* = reduction): a pair of nuclear divisions in quick succession, one of which is reductional. Four haploid nuclei are produced as a result of meiosis. (Figure 89E.)
- Meristogenous** (Gr. *meros* = part + *gennao* = I give birth): refers to the origin of a fruiting body from the division of a simple cell or of adjacent cells of the same hypha (Figure 139A).
- Merosporangium** (pl. *merosporangia*; Gr. *meros* = portion + *sporangium*): a cylindrical sporangium (Figure 67J).
- Microconidium** (pl. *microconidia*; Gr. *mikron* = small + *konis* = dust + *-idion*, dimin. suffix): a small conidium which often acts as a spermatium (Figures 113G, H).
- Microcytic** (Gr. *mikros* = small + *kyklos* = circle, cycle): short-cycled. Applied to those species of rusts which produce no binucleate spores other than teleutospores.

- Microcyst** (Gr. *mikros* = small + *kystis* = bladder): a small, encysted protoplast. Usually an encysted myxamoeba of the Myxomycetes or Acrasiales.
- Micron** (pl. microns or micra; Gr. *mikron* = small): a unit of measurement equal to 0.001 mm. or approx. $\frac{1}{25,000}$ inch.
- Monocentric** (Gr. *monos* = single + *kentron* = center): a thallus radiating from a single point at which a reproductive organ (sporangium or resting spore) is formed.
- Monokaryotic** (Gr. *monon* = alone, single + *karyon* = nut, nucleus): containing a single nucleus.
- Monomorphic** (Gr. *monos* = alone, one + *morphe* = form): producing one type of zoospore.
- Monophyletic** (Gr. *monon* = alone, single + *phylon* = stock, race): of a single line of descent.
- Monoplanetic** (Gr. *monos* = alone, only + *planetes* = wanderer): refers to a species which produces only one type of zoospore and in which there is but one swarming period.
- Mucormycosis**: a disease of animals or human beings caused by a member of the Mucorales.
- Mycelium** (pl. mycelia; Gr. *mykes* = mushroom, fungus): mass of hyphae constituting the body (thallus) of a fungus.
- Mycobiont** (Gr. *mykes* = fungus + *bios* = life): the fungous component of a lichen.
- Mycology** (Gr. *mykes* = mushroom, fungus + *logos* = discourse): the science which treats of fungi.
- Mycophagy** (Gr. *mykes* = mushroom + *phagein* = to eat): the eating of mushrooms.
- Mycorrhiza** (pl. mycorrhizae; Gr. *mykes* = mushroom + *rhiza* = root): an association between fungal hyphae and roots of higher plants, probably representing a condition of balanced parasitism through which, in some cases at least, the plant obtains nourishment from the fungal hyphae.
- Myxamoeba** (pl. myxamoebae; Gr. *myxa* = slime + *amoeba* = change): an amoeboid cell, particularly one of the Myxomycetes (Figures 26C, G).
- Nutriocyte** (L. *nutrio* = to nourish + Gr. *kystis* = bladder): the inflated portion of the ascogonium of *Pericystis*, which eventually develops into a spore cyst.
- Obligate parasite** (L. *obligare* = to bind; Gr. *parasitos* = table mate): an organism which can obtain food only from living protoplasm. Obligate parasites cannot be grown in culture on non-living media.
- Obligate saprobe** (L. *obligare* = to bind; Gr. *sapros* = rotten + *bios* = life): an organism which must obtain its food from dead organic matter, and is incapable of infecting another living organism.
- Ocellus** (pl. ocelli; L. *occulus* = eye): an eyespot functioning as a lens and concentrating the light rays on a photosensitive spot.
- Oidiophore** (Gr. *oidion* = small egg + *phoreus* = bearer): a hypha which fragments into oidia from the tip toward the base (Figure 151).
- Oidium** (pl. oidia; Gr. *oidion* = small egg): a thin-walled, free, hyphal cell derived from the fragmentation of a somatic hypha into its component cells, or from an oidiophore. It behaves as a spore or as a spermatium. (Figures 9A, 151.)
- Oidization** (Gr. *oidion* = small egg): the union of an oidium with a somatic hypha, resulting in the dikaryotization of the latter.

- Oögamous** (Gr. *oön* = egg + *gamos* = marriage, union): refers to a type of fertilization in which two heterogametangia come in contact, and the contents of one flow into the other through a pore or tube (Figure 15).
- Oögonium** (pl. oögonia; Gr. *oön* = egg + *gennao* = I give birth): a female gametangium containing one or more eggs (Figure 15).
- Oösphere** (Gr. *oön* = egg + *sphaira* = sphere): a large, naked, non-motile, female gamete (Figure 52A).
- Oöspore** (Gr. *oön* = egg + *sporos* = seed, spore): a thick-walled spore which develops from an oösphere through either fertilization or parthenogenesis (Figure 57J).
- Operculum** (pl. opercula; L. *operculum* = lid): a hinged cap on a sporangium or an ascus (Figures 44B, 87B).
- Ostiole** (L. *ostiolum* = little door): a neck-like structure in an ascocarp, lined with periphyses, and terminating in a pore. Also the opening of a pycnidium. (Figure 112.)
- Paraphyses** (sing. paraphysis; Gr. *para* = beside + *physis* = a being, a growth): sterile, basally attached structures in a hymenium (Figures 112, 148).
- Parasexuality** (Gr. *para* = beside + *sexuality*): a process in which plasmogamy, karyogamy, and haploidization take place in sequence, but not at specified points in the life cycle of an individual. Of significance in heterokaryotic individuals which derive some of the benefits of sexuality from a parasexual cycle.
- Parasite** (Gr. *parasitos* = eating beside another; from *para* = beside + *sitos* = wheat, food): an organism which lives at the expense of another, usually invading it and causing disease.
- Parthenogenesis** (Gr. *parthenos* = virgin + *genesis* = birth): the development of the normal product of sexual reproduction from the female gamete alone.
- Pellicle** (L. *pellis* = skin, dimin. form): a skin-like aggregation of bacteria or yeasts on the surface of liquid media. Any surface, skin-like growth.
- Penicillus** (pl. penicilli; L. *penicillum* = small brush): the conidiophore of the genus *Penicillium* (Figures 103C, D; 104).
- Peridiole** (Gr. *peridion* = small leather pouch + L. *-olum* = dimin. suffix): the glebal chamber of the Nidulariales, which has a hard, waxy wall of its own; contains the basidiospores, but acts as a propagating unit as a whole (Figure 193).
- Peridium** (pl. peridia; Gr. *peridion* = small leather pouch); the outside covering or wall of a fructification.
- Periphyses** (sing. periphysis; Gr. *peri* = around + *physis* = a being, a growth): short, hair-like growths in the form of a fringe lining the inside of an ostiole or of a pore in a stroma (Figures 112, 132L).
- Periplasm** (Gr. *peri* = around + *plasma* = a molded structure): a layer of protoplasm surrounding the oösphere of certain Oömycetes (Figure 55D).
- Perithecium** (pl. perithecia; Gr. *peri* = around + *theke* = a case): a closed ascocarp with a pore at the top, a true ostiole, and a wall of its own (Figure 85C).
- Petri dish** (named after R. J. Petri, a German scientist): a glass container consisting of a circular, flat dish with vertical sides, and a similar but slightly larger cover which fits over it. Standard equipment for the growth of microorganisms in pure culture.

- Phaneroplasmodium** (pl. *phaneroplasmodia*; Gr. *phaneros* = visible + *plasmodium*): a plasmodium consisting of a well-differentiated advancing fan and conspicuous thick strands in which ecto- and endoplasmic regions are well differentiated, and in which the protoplasm is coarsely granular. Characteristic of the Physarales (Figure 32).
- Phialid** (Gr. *phialis* = phial): a small bottle-shaped structure from which spores are produced. The latter are characteristically formed inside the phialid and extruded.
- Phialospore** (Gr. *phialis* = phial + *sporos* = seed, spore): a spore produced from a phialid.
- Phycobiont** (Gr. *phykos* = alga + *bios* = life): the algal component of a lichen.
- Pileus** (pl. *pilei*; L. *pileus* = cap): upper portion or cap of certain types of ascocarps and basidiocarps (Figures 126, 180).
- Planogamete** (Gr. *planetes* = wanderer + *gametes* = husband, sex cell): a motile gamete (Figures 14A, B, sperm in C).
- Planogametic copulation** (Gr. *planetes* = wanderer + *gametes* = husband; L. *copulare* = to couple): fusion of naked gametes, one or both of which are motile (Figure 14).
- Plasmodiocarp** (Gr. *plasma* = a molded object + *karpos* = fruit): a curved or branched, vein-like fruiting structure of some of the Myxomycetes (Figure 36).
- Plasmodium** (pl. *plasmodia*; Gr. *plasma* = a molded object): a naked, multinucleate mass of protoplasm moving and feeding in amoeboid fashion. The somatic phase of the Myxomycetes and the Plasmodiophoromycetes (Figures 30, 31, 32, 64E, M; 65E, M).
- Plasmogamy** (Gr. *plasma* = a molded object + *gamos* = marriage, union): the fusion of two protoplasts (Figures 15, 18).
- Plectenchyma** (Gr. *pleko* = I weave + *enchyma* = infusion, i.e., a woven tissue): the general term employed to designate all types of fungal tissues. The two most common types of tissues are prosenchyma and pseudoparenchyma. (Figure 7.)
- Polycentric** (Gr. *polys* = much, many + *kentron* = center): a thallus radiating from many centers at which reproductive organs (sporangia or resting spores) are formed.
- Polyphyletic** (Gr. *poly* = much, many + *phylon* = stock, race): of several lines of descent.
- Polyplanetic** (Gr. *polys* = much, many + *planetes* = wanderer): refers to a species in which there are several swarming periods but only one type of zoospore.
- Porospore** (Gr. *poros* = pore + *sporos* = seed, spore): a spore produced from pores of a conidiophore.
- Primordium** (pl. *primordia*; L. *primordium* = beginning): the beginning stage of any structure.
- Probasidium** (pl. *probasidia*; Gr. *pro* = before + *basidium*): a binucleate hyphal cell which may undergo morphological changes before developing into a mature basidium (Figure 157).
- Progametangium** (pl. *progametangia*; Gr. *pro* = before + *gametangium*): a cell which gives rise to a gametangium (Figure 70E).
- Promycelium** (pl. *promycelia*; Gr. *pro* = before + *mycelium*): the epibasidium of the rusts and smuts. A germ tube issuing from the teleutospore, which bears the basidiospores. (Figures 164R, A.)

- Prosenchyma** (Gr. *pros* = toward + *enchyma* = infusion, i.e., approaching a tissue): a type of plectenchyma in which the component hyphae lie parallel to one another and are easily recognized as such (Figure 7A).
- Prosorus** (pl. *prosori*; Gr. *pro* = before + *soros* = heap): a structure which eventually divides to give rise to a sorus (Figure 42D).
- Protista** (Gr. *protiston* = the very first): a kingdom proposed by Haeckel in an attempt to classify organisms showing characteristics of both plants and animals.
- Protoperithecium** (pl. *protoperithecia*; Gr. *protos* = first + *perithecium*): a perithecial initial which develops into a perithecium after fertilization has occurred.
- Protoplasmodium** (pl. *protoplasmodia*; Gr. *protos* = first + *plasmodium*): a microscopic plasmodium, with no differentiated fan-shaped region or strands, which exhibits slow and irregular streaming and gives rise to but a single, minute fruiting body. Typical of the Echinosteliales, but occurring in other Myxomycetes as well (Figure 30).
- Pseudocapillitium** (pl. *pseudocapillitia*; Gr. *pseudo* = false + *capillitium*): irregular threads, plates, or other structures present among the spores within the fructifications of many Myxomycetes; resembles capillitium.
- Pseudomycelium** (pl. *pseudomycelia*; Gr. *pseudo* = false + *mycelium*): a series of cells adhering end to end to form a chain. Produced by some yeasts. (Figure 92.)
- Pseudoparaphyses** (sing. *pseudoparaphysis*; Gr. *pseudo* = false + *paraphysis*): sterile threads attached both to the roof and to the base of an ascocarp (Figure 134H).
- Pseudoparenchyma** (pl. *pseudoparenchymata*; Gr. *pseudo* = false + *parenchyma* = a type of plant tissue): a type of plectenchyma consisting of oval or isodiametric cells, the component hyphae having lost their individuality (Figure 7B).
- Pseudoperithecium** (pl. *pseudoperithecia*; Gr. *pseudo* = false + *perithecium*): a uniloculate ascostroma (Figures 132L, M).
- Pseudoplasmodium** (pl. *pseudoplasmodia*; Gr. *pseudo* = false + *plasmodium*): an aggregation of amoeboid cells constituting the initial stage of fruiting of the Acrasiales (Figures 21A-E).
- Pseudoseptum** (pl. *pseudosepta*; Gr. *pseudo* = false + L. *septum* = hedge): a plug-like partition of cellulose or other substance in a hypha, resembling a septum.
- Pseudospore** (Gr. *pseudo* = false + *sporos* = seed, spore): a non-motile naked spore. Found in some Acrasiales.
- Pseudothecium**: contraction of pseudoperithecium.
- Pycnidiospore** (*pycnidium* + Gr. *sporos* = seed, spore): a conidium borne in a pycnidium (Figures 133B, 140).
- Pycnidium** (pl. *pycnidia*; Gr. *pyknon* = concentrated + *-idion*, dimin. suffix): an asexual, hollow fruiting body, lined inside with conidiophores (Figures 80A, 138).
- Pycniospore** (Gr. *pyknos* = concentrated + *sporos* = seed, spore): the old designation for the spermatium of the rusts, used before the true function of the spermatia was discovered (Figure 160).
- Pycnium** (pl. *pycnia*; Gr. *pyknon* = concentrated): the old designation for the spermogonium of the rusts (Figure 160).

- Pycnosclerotium** (pl. *pycnosclerotia*; *pycnidium* + *sclerotium*, from Gr. *skleron* = hard): a more or less hard-walled structure resembling a pycnidium but containing no spores (Figure 133D).
- Reproduction** (L. *re* = prefix for again + *producere* = to bring forth): the production of new individuals having all the characteristics typical of the species.
- Resupinate** (L. *resupinatus* = inverted): lying flat on the substratum with the hymenium on the free surface.
- Reticulate** (L. *reticulum* = a small net): having the form of a net; covered with net-like ridges (Figure 27C).
- Rhizoid** (Gr. *rhiza* = root + *-oeides* = like): a short, thin branch of a thallus, superficially resembling a root (Figure 43A).
- Rhizomorph** (Gr. *rhiza* = root + *morphe* = shape): a thick strand of somatic hyphae in which the hyphae have lost their individuality, the whole mass behaving as an organized unit. The structure of the growing tip of the rhizomorph somewhat resembles that of a root tip: hence the name.
- Rhizomycelium** (pl. *rhizomycelia*; Gr. *rhiza* = root + *mycelium*): a rhizoidal system extensive enough to resemble mycelium superficially (Figure 44A).
- Rhizoplast** (Gr. *rhiza* = root + *plastid*): a connecting strand between the nucleus and the blepharoplast.
- Saprobe** (Gr. *sapros* = rotten + *bios* = life): an organism which utilizes dead organic matter for food.
- Sclerotium** (pl. *sclerotia*; Gr. *skleron* = hard): a hard resting body resistant to unfavorable conditions, which may remain dormant for long periods of time and germinate upon the return of favorable conditions (Figures 8C, D).
- Scoleospore** (Gr. *skolex* = worm + *sporos* = seed, spore): an elongated, needle- or worm-like spore (Figure 142H).
- Self-compatible** (L. *compati* = to suffer with): self-fertile. Refers to a thallus which reproduces sexually by itself.
- Self-incompatible** (L. *in* = not + *compati* = to suffer with): self-sterile. Refers to a thallus which cannot reproduce by itself sexually.
- Septate** (L. *septum* = hedge): with cross-walls (Figure 2B).
- Septum** (pl. *septa*; L. *septum* = hedge, partition): a cross-wall in a hypha (Figure 2B).
- Seta** (pl. *setae*; L. *seta* = bristle): a bristle-like hair (Figures 141B, 142F, G).
- Sexual reproduction**: reproduction involving the fusion of two compatible nuclei.
- Sirenin** (Gr. *sirein* = siren): a reproductive hormone secreted by the female gametes of *Allomyces* which attracts the male gametes.
- Slime mold**: a member of the class Myxomycetes (Figures 25–40).
- Soma** (pl. *somata*; Gr. *soma* = body): the body of an organism as distinguished from its reproductive organs or reproductive phase.
- Somatic** (Gr. *soma* = body): refers to the body phase—in plants, the vegetative phase—structure, or function as distinguished from the reproductive.
- Somatogamy** (Gr. *soma* = body + *gamos* = marriage, union): fusion of somatic cells during plasmogamy (Figure 18).
- Sorocarp** (Gr. *soros* = heap + *karpos* = fruit): the fructification of the Acrasiales (Figures 19, 21A).
- Sorus** (pl. *sori*; Gr. *soros* = heap): a mass of sporangia or spores.

Species (sing. and pl. *species*; L. *species* = kind): the unit of classification.

A group of closely related individuals resembling one another in certain inherited characteristics. It is designated by a binomial consisting of the generic name and the specific epithet.

Spermatiophore (Gr. *spermaton* = little seed + *phoreus* = bearer): a specialized hypha which produces spermatia (Figures 120D, 121F).

Spermatium (pl. *spermatia*; Gr. *spermaton* = little seed): a non-motile, uni-nucleate, spore-like male structure which empties its contents into a receptive female structure during plasmogamy. Spermatia are variously regarded as gametes or gametangia. (Figures 17A, C; 132D, F; 164F, G.)

Spermatization (Gr. *sperma* = seed): plasmogamy by the union of a spermatium with a receptive structure (Figures 17C, D).

Spermogonium (pl. *spermogonia*; Gr. *sperma* = seed, *sperm* + *gennao* = I give birth): a structure resembling a pycnidium and containing minute, rod-shaped, or oval spore-like bodies which in some cases have proved to be functional spermatia (Figures 132D, 133E, 164D).

Sphaerocyst (Gr. *sphaira* = sphere + *kystis* = bladder): spherical cells present in the trama of the Russulaceae (Figure 182D).

Sporangiolum (pl. *sporangiola*; Gr. *sporos* = seed, *spore* + *angeion* = vessel + L. *-olum*, dimin. suffix): a small sporangium containing few spores (Figures 66B, D).

Sporangiophore (Gr. *sporos* = seed, *spore* + *angeion* = vessel + *phoreus* = bearer): a hypha which bears a sporangium (Figures 59, 70B, B').

Sporangiospore (Gr. *sporos* = seed, *spore* + *angeion* = vessel + *sporos*): a spore borne within a sporangium (Figures 43B, 70C, C').

Sporangium (pl. *sporangia*; Gr. *sporos* = seed, *spore* + *angeion* = vessel): a sac-like structure, the entire protoplasmic contents of which become converted into an indefinite number of spores (Figures 34, 49A).

Spore (Gr. *sporos* = seed, *spore*): a minute propagative unit functioning as a seed, but differing from it in that a spore does not contain a preformed embryo (Figure 12).

Sporocladium (pl. *sporocladia*; Gr. *sporos* = seed, *spore* + *klados* = branch): a special type of fertile branch of a sporangiophore which bears merosporangia (Figure 67C).

Sporocyte (Gr. *sporos* = seed, *spore* + *kytos* = hollow vessel): a structure containing spores. See Labyrinthulales, page 61.

Sporodochium (pl. *sporodochia*; Gr. *sporos* = seed, *spore* + *docheion* = container): a cushion-shaped stroma covered with conidiophores (Figures 72C, 116C, 146A).

Sporophore (Gr. *sporos* = seed, *spore* + *phoreus* = bearer): any structure which bears spores.

Sporothallus (pl. *sporothalli*; Gr. *sporos* = seed, *spore* + *thallos* = shoot, thallus): a thallus which produces spores, as opposed to a gametothallus (Figure 45I).

Sterigma (pl. *sterigmata*; Gr. *sterigma* = support): a small hyphal branch or structure, which supports a sporangium, a conidium, or a basidiospore (Figures 59A, 100A, 149E).

Stroma (pl. *stromata*; Gr. *stroma* = mattress): a compact somatic structure, much like a mattress, on which or in which fructifications are usually formed (Figures 8A, B).

- Stylospore** (Gr. *stylos* = pilar + *sporos* = seed, spore): an elongated or cane-shaped pycnidiospore of unknown function (Figure 140C).
- Subiculum** (pl. subicula; L. dimin. of *subex* = underlayer): a loose hyphal mat on or in which fruiting bodies are formed.
- Suboperculate** (L. *sub* = under + *operculum* = small door): an ascus with a thick apical ring capped by a plug or hinged operculum.
- Swarm cell**: a flagellated cell. Usually applied to the motile cells of the Myxomycetes and the Plasmodiophoromycetes (Figures 26D, 29, 64C).
- Symphogenous** (Gr. *synphyein* = to grow together + *gignesthai* = to be born, i.e., originating from structures which grow together): refers to the origin of a fruiting body from a number of interweaving hyphae (Figure 139C).
- Synnema** (pl. synnemata; Gr. *syn* = together + *nema* = yarn): a group of conidiophores cemented together and forming an elongated spore-bearing structure (Figure 80D).
- Taxonomy** (Gr. *taxis* = order, arrangement + *nomos* = law): the science of classification.
- Teleutospore** (Gr. *teleutaios* = last + *sporos* = seed, spore): a thick-walled resting spore in some Heterobasidiomycetidae, notably the rusts and smuts, in which karyogamy occurs; it is a part of the basidial apparatus (Figures 164P, Q).
- Telium** (pl. telia; Gr. *telos* = end): a group of binucleate cells which produce teleutospores (Figure 164O).
- Tetrapolarity** (Gr. *tetras* = a group of four + *polos* = pole): a condition of sexual compatibility in some Basidiomycetes in which each of the four basidiospores of a basidium is of a different strain.
- Thallophyte** (Gr. *thallos* = shoot, thallus + *phyton* = plant): a plant whose somatic phase is devoid of stems, roots, or leaves, and which propagates by means of spores.
- Thallus** (pl. thalli; Gr. *thallos* = shoot): a relatively simple plant body devoid of stems, roots, and leaves; in fungi, the somatic phase.
- Trama** (pl. tramae; L. *trama* = woof): the fungal tissue composing the pileus or bearing the hymenium of the Homobasidiomycetidae (Figure 182).
- Trichogyne** (Gr. *thrix* = hair + *gyne* = woman, female): the receptive neck of the ascogonium, which is often long and hair-like (Figures 17B, 82A, 113F).
- Trophocyst** (Gr. *trophe* = food + *kystis* = bladder): an enlarged cell. The swollen portion of the sporangiophore of *Pilobolus* (Figure 68).
- Unitunicate** (L. *unus* = one + *tunica* = coat, mantle): an ascus in which both the inner and outer wall are more or less rigid and do not separate during spore ejection.
- Universal veil**: a thin, veil-like membrane which covers certain types of young mushrooms. Upon expansion of the mushroom, the universal veil tears and its remnants may be seen in the form of scales on the pileus and in the form of a volva. (Figures 181, 185.)
- Uredium** (pl. uredia; L. *urere* = to burn): a group of binucleate cells which give rise to uredospores (Figure 162).
- Uredospore** (L. *urere* = to burn + Gr. *sporos* = seed, spore): a binucleate, repeating spore of the Uredinales (Figure 164M).
- Vesicle** (L. *vesicula* = small bladder): a thin, bubble-like structure in which zoospores are released or are differentiated; also the bulbous head terminating the conidiophore of *Aspergillus* (Figures 57C, 61L, 100).

- Volva** (pl. *volvae*; L. *volva* = covering): a cup at the base of the stem of certain mushrooms (Figure 181).
- Zoösporangium** (Gr. *zoön* = animal + *sporangium*): a sporangium which contains zoöspores (Figures 45I, 65G).
- Zoöspore** (Gr. *zoön* = animal + *sporos* = seed, spore): a motile, asexually produced spore (Figures 45J, K; 61E).
- Zygophore** (Gr. *zygos* = yoke + *phoreus* = bearer): a specialized hyphal branch bearing zygospores (Figure 72B).
- Zygosporangium** (pl. *zygosporangia*; Gr. *zygos* = yoke + *sporangium*): a sporangium which contains a zygospore (Figure 75E).
- Zygospore** (Gr. *zygos* = yoke + *sporos* = seed, spore): a resting spore which results from the fusion of two gametangia in the Zygomycetes (Figures 16, 71).
- Zygote** (Gr. *zygos* = yoke): a diploid cell resulting from the union of two haploid cells (Figure 41H).

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